Inter-ocular Suppression and Sensory Eye Dominance in Human Vision

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Abstract

Inter-ocular interactions are a crucial component of binocular vision, providing important insights into how the inputs from the two eyes are combined and compete with each other. This aspect was addressed in a series of psychophysical experiments by investigating inter-ocular suppression and sensory eye dominance in the normal visual system. Firstly, patterns of individual differences, and variations in sensory eye dominance, in terms of susceptibility to binocular rivalry (BR) and continuous flash suppression (CFS), were established in a representative sample of participants. The results indicate that there may be a common mechanism underpinning these inter-ocular suppression phenomena, whilst sensory eye dominance associated with depth of suppression may be task dependent. Furthermore, this thesis has also demonstrated the adjustment of sensory eye dominance following short periods of monocular deprivation/distortion in the adult visual system. Crucially, it has been shown that changes in sensory eye dominance resulted specifically from reduced inter-ocular suppression of the previously treated eye. Moreover, the present findings underscore a role of inter-ocular imbalance in the visual processing, arising from both low-level sensory input and higher-level processes, in altering subsequent sensory eye dominance. Taken together, the findings of this thesis imply that there is a mechanism that detects inter-ocular conflict, which in turn elicits inter-ocular inhibition that is sensitive to imbalance between the two eyes' processing. These findings have contributed new knowledge to the understanding of inter-ocular interactions, and placed important constraints on the models of binocular vision.

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List of publications

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Chapter 1

General introduction

1.1 Fundamentals of binocular vision

Two eyes with overlapping visual fields are one of the hallmarks of the mammalian visual system and enable the three-dimensional structure of the visual environment to be perceived via processes such as stereopsis (Howard & Rogers, 1995). The monocular input to each of the eyes, projects to separate retinae, but then interacts at multiple stages of visual processing, such that the visual response to binocular stimulation is distinct from that when only one eye is stimulated (Pettigrew, 1991). Retinal neurons only respond to input to the corresponding eye and hence have monocular receptive fields. The earliest binocular interactions have been observed in the lateral geniculate nucleus (LGN), and can be either inhibitory or excitatory (e.g. Pettigrew, 1991; Sanderson, Bishop, & Darian-Smith, 1971; Sanderson, Darian-Smith, & Bishop, 1969; Schroeder, Tenke, Arezzo, & Vaughan, 1990; Sengpiel, Blakemore, & Harrad, 1995; Singer, 1970). At the level of the cortex the majority of neurons are binocularly sensitive and respond to input from either eye (Hubel & Wiesel, 1962).

According to Worth's (1903) classification, the first grade of binocular vision is simultaneous macular perception. It refers to the ability of the visual system to perceive separate images presented to the two eyes at the same time. Given the substantial overlap in the extent of visual fields, the corresponding regions of the two retinae receive inputs from virtually identical locations in the environment. The ability to unify these inputs from both eyes into a single representation forms the second grade of binocular vision, namely fusion. This requires sensory unification of the two retinal images, as well as the motor coordination of the two eyes, such that sensory fusion can be maintained. The correspondence problem (i.e. matching the appropriate features belonging to the same object in the two eyes), however, is not straightforwardly solved as the two eyes capture images from the external world slightly differently due to their physical horizontal separation. The small spatial offset between images viewed by the two eyes is referred to as binocular disparity (Howard & Rogers, 1995). Fusion can only take place when this disparity is within a certain range, referred to as the Panum's fusional area (Figure 1.1; Mitchell, 1966). Once binocular fusion is attained (by solving the correspondence problem), binocular disparity is an essential cue that codes stereoscopic depth information.

In some circumstances the fixation points for the two eyes can be different. For instance, strabismus, a condition where the patient is not able to align the axes of the two eyes properly, that is, they point in different directions (von Noorden & Campos, 2001). Here, a given object in the visual space falls on the non-corresponding locations in the two retinae, resulting in substantial binocular disparity which exceeds the limits of Panum's Area. Fusion fails because the brain is unable to resolve such a large offset to achieve binocular correspondence, giving rise to visual confusion or

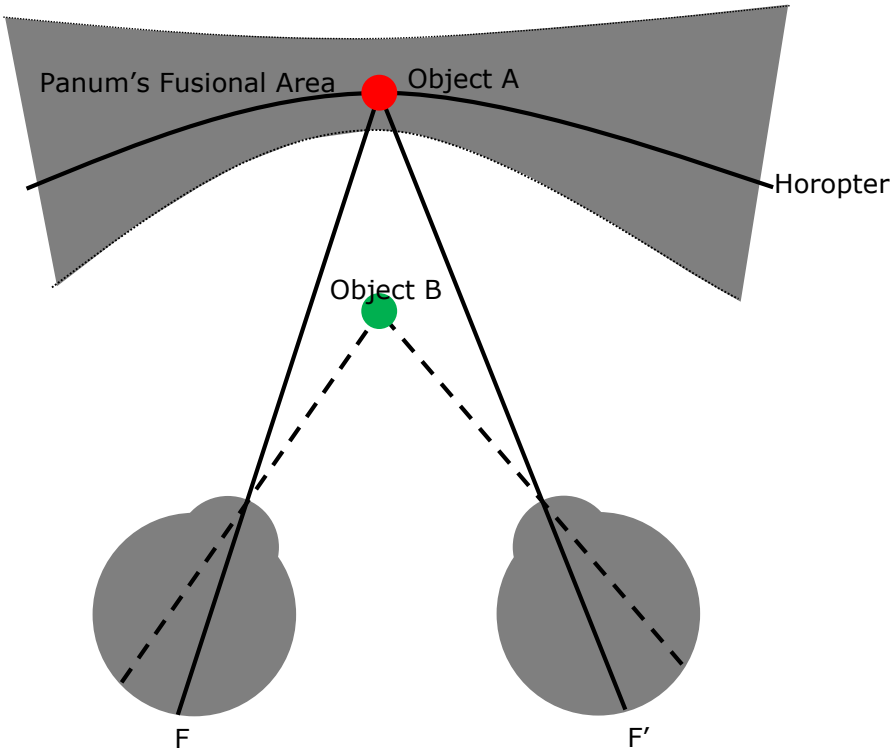


Figure 1.1: A cartoon illustration of Panum's fusional area. This is the top view of the eyes viewing objects A (red dot) and B (green dot). The horizontal curve on the top marks the horizontal horopter, where all points falling on this curved-line have the same zero disparity as fixation. The shaded area around the horopter is Panum's fusional area, inside which the objects have a disparity within a tolerable range that supports a unified percept. The eyes are fixating on the object A, so that the light from object A fall on the foveae—points F and F' in the diagram. A single percept of object A can be achieved because it is within Panum's fusional area for the two retinal images to be fused. However, the object B produces a disparity outside the fusional range, leading to physiological diplopia. Image created on the basis of the illustrations by Patterson (2015).

diplopia (i.e. double vision). In addition to the case of disparate retinal locations stimulated by the same object, failure of fusion can result from a more extreme situation where the entire images can be distinct in the two eyes (i.e. different objects stimulate the corresponding locations in the two retinae). Although relatively rare in real life, consider a situation where one eye's view is occluded by a wall, while the other eye sees the scene behind the wall. Binocular correspondence cannot be achieved because of the lack of correlation between the two images (Blake & Boothroyd, 1985). Under both conditions stated above, binocular fusion is not achieved and the visual system has to resolve the conflict by adopting a strategy to prevent the unwanted consequences of confusion and diplopia (e.g. Georgeson & Wallis, 2014). This thesis will focus on the latter case, whereby the inter-ocular conflict arises from discrepancies in the spatial content of the two eyes' images such that they are uncorrelated.

It has long been recognised that one effective solution to inter-ocular conflict in visual input is to alternate visual awareness between the two images, known as binocular rivalry (W. J. M. Levelt, 1965). Another way to resolve the conflict is (prolonged) inter-ocular suppression, whereby the image viewed by one eye dominates perception by suppressing the image in the other eye but not vice versa (e.g. Tsuchiya & Koch, 2005). Physiological evidence suggested that cell responses to a stimulus viewed by the ipsilateral eye were reduced in cat striate cortex, when a conflicting stimulus was presented to the contralateral eye. This is in contrast with the binocular facilitation found when the two eyes' images were matched in spatial content (Sengpiel et al., 1995). This led Sengpiel and colleagues to conclude that the conflict between the two eyes' images is resolved through inter-ocular suppression. The term inter-ocular suppression can sometimes refer to the

inhibitory effects on one eye's response produced by the input from the other eye, including conditions that have an absence of inter-ocular conflict (e.g. Meese, Georgeson, & Baker, 2006). Nonetheless, inter-ocular suppression mentioned in this thesis will denote, unless otherwise stated, the perceptual suppression of one eye's image to resolve conflict between the two eyes.

1.2 Binocular rivalry

Binocular rivalry (BR) is a process that resolves conflict when the images viewed by the eyes are too dissimilar to be fused. Random perceptual alternations are experienced, and typically, only one of the images (i.e. the dominant image) is perceived at a time (W. J. M. Levelt, 1965). The other is temporarily erased from awareness, appearing invisible to the observer.

Systematic study of BR has been enabled by the invention of the mirror stereoscope by Wheatstone (1838). The device is designed to project independent images onto the corresponding positions of the two eyes' retinae simultaneously, a technique known as dichoptic presentation. An example of stimuli commonly used to trigger BR is a pair of orthogonally-oriented sinusoidal gratings (Blake, 2001). The use of basic visual stimuli in BR research (and other types of inter-ocular suppression) enables investigations of low-level visual processing, whereas more complex stimuli (e.g. face and house images) are often employed to explore higher-level visual functions. The present research focuses on relatively low levels of visual processing, using stimuli that are well controlled (specified in spatial frequency, luminance contrast, exposure duration, etc.) and commonly used in conventional psychophysical studies.

Among the fluctuations of dominance that occur during rivalry, a single

perceptual phase before perception switches can last up to a few seconds. The distribution of these durations is positively skewed such that brief dominance periods are most frequent compared to longer phases (Figure 1.2). Dominance durations can be well characterised by a gamma or log-normal distribution[1] (e.g. Lehky, 1995; N. J. Wade, 1975). The temporal dynamics of BR are nonetheless stochastic (Blake, Fox, & McIntyre, 1971; Fox & Herrmann, 1967; W. J. M. Levelt, 1965; Walker, 1975). There is little predictability for initial dominance at the onset of rivalry, given that the two rivalrous stimuli are visually of the same strength (i.e. one is not more salient than the other, as in a pair of gratings merely differing in orientations). Moreover, the dominance/suppression phase durations during rivalry appear to be completely random and sequentially independent; the duration for each single phase is not correlated with the previous or subsequent one (Fox & Herrmann, 1967; Walker, 1975; but see Section 1.6.3). In addition, whilst it is commonly assumed that only one of the stimuli is perceived at a time during BR (i.e. exclusive dominance), a mixture of both stimuli is not an unusual perceptual occurrence (Figure 1.3; Meenes, 1930). A mixed percept is typically referred to as that appearing to consist of intermingled portions from both stimuli, such that they are both partially visible in complementary fashion at the same time (i.e. piecemeal). However a less common type of mixed percept may also occur, namely superimposition, where all part of each stimulus is perceived in complete form, and the two appear to spatially overlap in the visual field. Some researchers tend to treat mixed percepts as transitions between the two exclusive percepts and

[1]More recent studies have shown that this might be a common feature for bistable perception, including phenomena that do not involve inter-ocular conflict such as Necker cube perception (Borsellino, de Marco, Allazetta, Rinesi, & Bartolini, 1972; Brascamp, van Ee, Pestman, & van den Berg, 2005; Leopold & Logothetis, 1999; Long & Toppino, 2004).

often exclude them from analysis. However, sustained experience of mixed perception during BR is likely to be the case (e.g. Klink, Brascamp, Blake, & Van Wezel, 2010) and systematic individual differences in susceptibility to mixed percepts have also been reported (e.g. Antinori, Carter, & Smillie, 2017). More importantly, not only is the probability of mixed percepts influenced by stimulus properties such as contrast and spatial frequency (Blake, Yu, Lokey, & Norman, 1998; Hollins, 1980; Hollins & Hudnell, 1980; Katyal, Engel, He, & He, 2016; O'Shea, Sims, & Govan, 1997; Y. Yang, Rose, & Blake, 1992), but it is thought to be inversely related to the depth of suppression engaged (Klink et al., 2010; van Loon et al., 2013). For these reasons, it is good practice and prudent to allow a third response type to indicate mixed perception, or ensure the exclusivity of perception when a mixed percept is unwanted.

Presenting an eye with a stimulus that is in conflict with another stimulus presented to the other eye, led to weaker cell response in cat's LGN and striate cortex compared to monocular stimulation, indicating a neural substrate for inhibitory inter-ocular interaction (Sengpiel et al., 1995; Sengpiel & Vorobyov, 2005). The observed physiological inter-ocular suppression is likely to be responsible for perceptual suppression during BR. In support of this idea, rivalry-related modulations have been revealed in LGN and early visual areas (in monkeys and humans), such that neural events were correlated with perceptual states during BR (Haynes, Deichmann, & Rees, 2005; Haynes & Rees, 2005; S.-H. Lee, Blake, & Heeger, 2005; Leopold & Logothetis, 1996; Polonsky, Blake, Braun, & Heeger, 2000; Wunderlich, Schneider, & Kastner, 2005). For example, it has been shown in an fMRI study that the BOLD signals in voxels (in LGN and V1) with left-eye (or right-eye) preferences were high during the left (or right) eye dominance

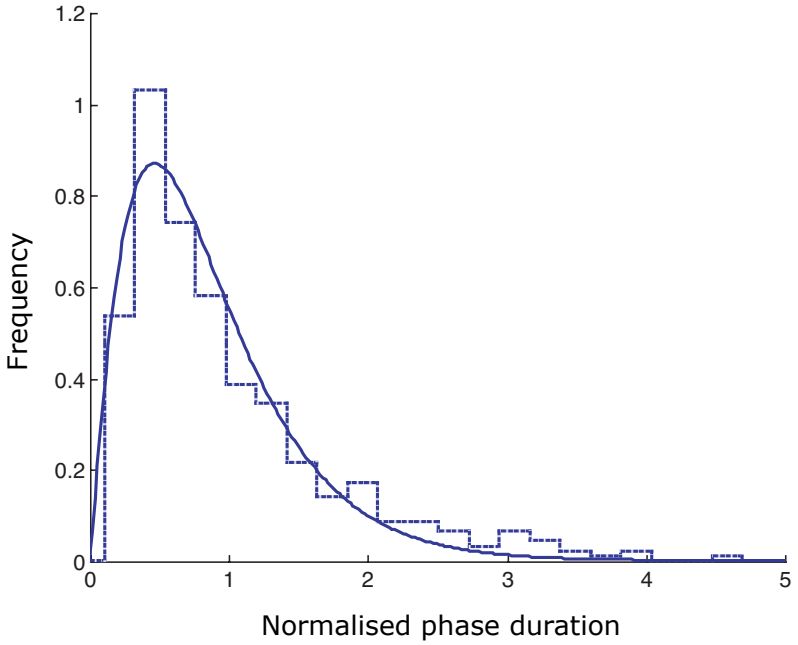


Figure 1.2: A typical example of distribution of (normalised) durations for dominance phases during binocular rivalry, as shown by the data in Mamassian and Goutcher (2005). This distribution is well estimated by a gamma function depicted as the continuous line. Figure adapted from Mamassian and Goutcher (2005).

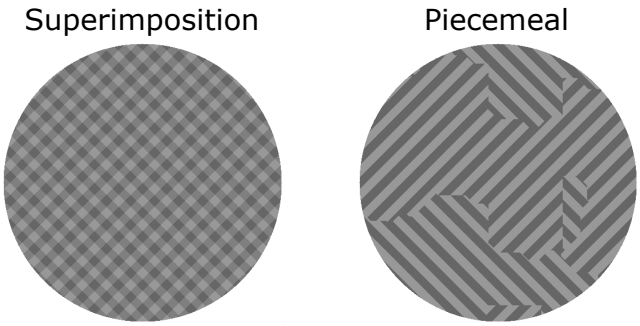


Figure 1.3: Examples of mixed percepts during binocular rivalry between a pair of orthogonally-oriented square wave gratings. It can be either piecemeal (right) or superimposition (left).

phase but decreased after the percept switched to the right (or left) eye's stimulus (Figure 1.4; Haynes et al., 2005).

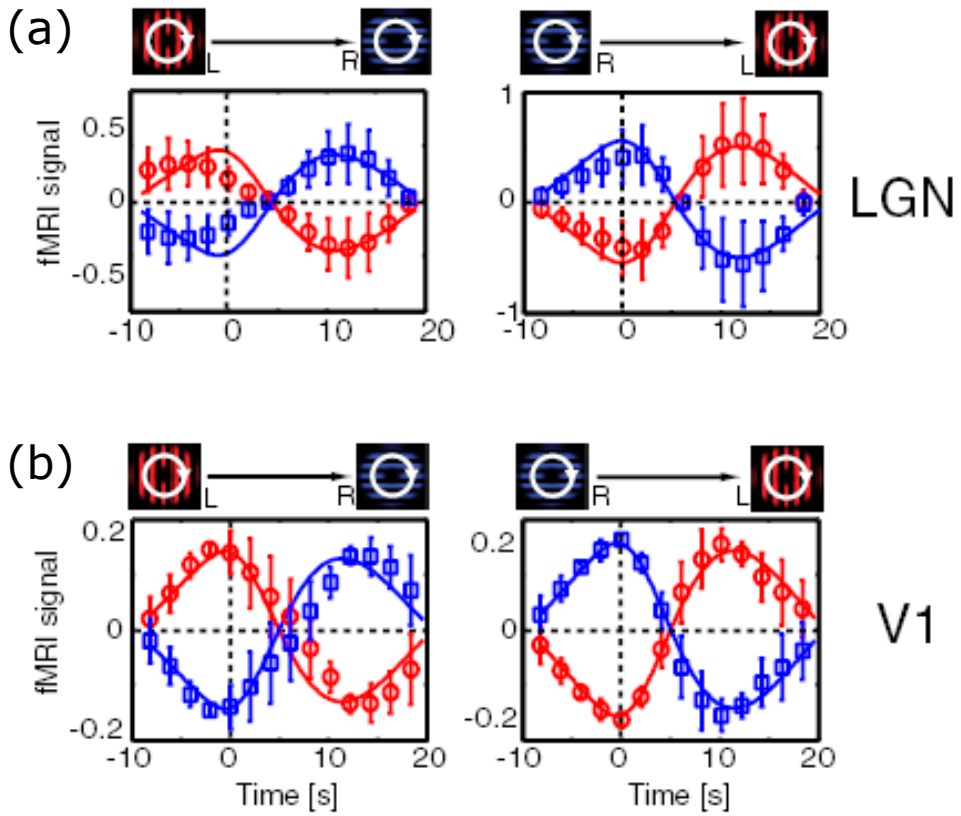


Figure 1.4: Evidence from an fMRI study showing neural correlates of BR in human LGN and primary visual cortex (V1). A pair of rotating gratings that oriented orthogonally were presented dichoptically to induce BR and the perceptual states (red vs. blue grating) were recorded continuously during fMRI measurements. The figure shows the time course of BOLD signals in voxels with left-eye preferences (red) and those with right-eye preferences (blue) during perceptual switches. The direction of switches is shown at the top of each graph. It can be seen that the BOLD signals were clearly correlated with perceptual dominance for both responses at (a) LGN and (b) V1. Adapted from Haynes et al. (2005).

1.3 Continuous flash suppression

Conflicting inputs from the two eyes may also be resolved by inter-ocular suppression, whereby a single percept is attained through sustained suppression of the image viewed by one eye. This is distinct from BR as perceptual alternations are not a characteristic. It should be noted, however, that some degree of, albeit modest, inter-ocular suppression is presumably involved when the two images rival (e.g. Tsuchiya, Koch, Gilroy, & Blake, 2006; Wales & Fox, 1970). To avoid confusion, hereafter binocular rivalry will refer specifically to the phenomenon of perceptual fluctuation between the two eyes' images, and crucially it will be regarded as a form of inter-ocular suppression only when the depth of suppression is measured.

One of the most striking forms of inter-ocular suppression is called continuous flash suppression (CFS), and has captured the attention of researchers since it was first introduced by Tsuchiya and Koch (2005). Under a CFS protocol, a dynamic visual stimulus (e.g. a changing Mondrian pattern) is presented to one eye, whilst another less "salient" target, often static, is presented to the other eye at the corresponding retinal position (see Figure 1.5). Critically, this dichoptic presentation, with substantial inter-ocular conflict, renders the target stimulus invisible to the observer, for periods of up to several minutes.

Originally Tsuchiya and Koch (2005) set out to infer the neuronal site for negative afterimage's formation by examining the effect of inter-ocular suppression on the strength of afterimages. If it is a central process (i.e. at cortical level), a reduction in strength of the afterimages is expected when they are formed in the presence of suppression. When BR was used to induce inter-ocular suppression, afterimages remained unaffected by sup-

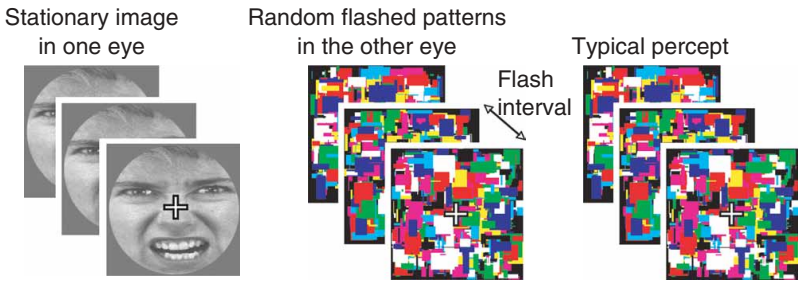


Figure 1.5: An example sequence of CFS used by Tsuchiya and Koch (2005). A dynamic Mondrian pattern is presented to one eye whilst a static face is shown to the other eye simultaneously. The Mondrian pattern is replaced with a random new pattern every 100 ms. The face image in this case is typically suppressed from awareness and only the Mondrian pattern is perceived. Image from Tsuchiya and Koch (2005).

pression (Lack, 1978). Although a pre-cortical origin might be implied, an alternative account could be that the relatively weak suppression rendered by BR did not influence the formation. This interpretation is supported by the observation of reduced afterimages when CFS was employed instead (Figure 1.6), which yielded suppression at least 10-fold higher in magnitude than that evoked by BR (Tsuchiya & Koch, 2005).

In addition to the more potent degree of suppression, the advantage of CFS over BR is that it produces consistent unilateral suppression, from the flashing stimulus viewed by one eye to the target presented to the other eye, rather than reciprocal suppression between eyes. Also noted by Tsuchiya and Koch was that the incidence of mixed percepts is much reduced with CFS (also see E. Yang, Blake, & McDonald, 2010), indicating more complete suppression. All these properties allow CFS to exert more reliable control over visual awareness of a specific stimulus, which is difficult to realise with BR because perception is unstable and subject to mixed percepts.

Like BR, inter-ocular suppression evoked by CFS has also been linked to early visual areas (Yamashiro et al., 2014; Yuval-Greenberg & Heeger, 2013).

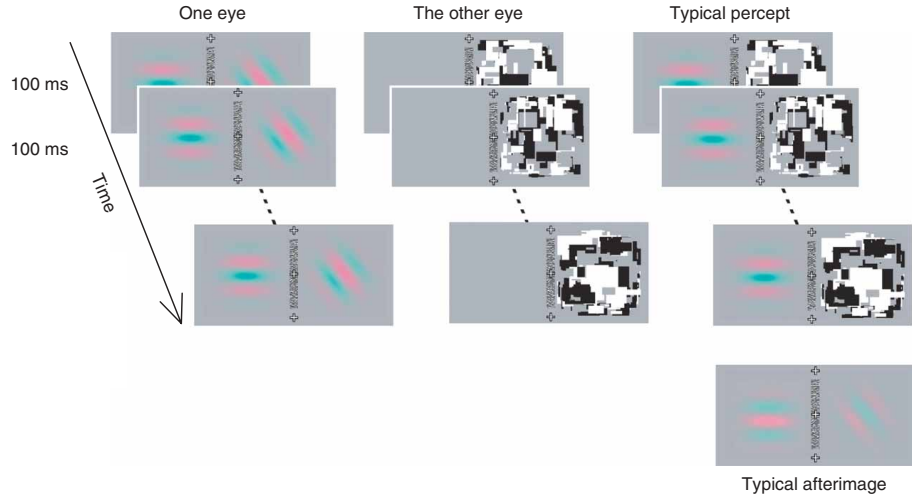


Figure 1.6: CFS impedes afterimage formation. Two identical adaptors (Gabor patches) were presented to one eye, one to each side of fixation, while a CFS stimulus (a Mondrian pattern) updated every 100 ms was presented to one side of fixation (right in this diagram) in the other eye. Following a 5-s adaptation period, the stimuli were removed and subjects reported the afterimage on the side where the CFS stimulus was previously presented being weaker compared to that on the other side on over 80% of the trials. Adapted from Tsuchiya and Koch (2005).

In Yuval-Greenberg and Heeger's (2013) study, reduced fMRI activity in V1, V2 and V3 was observed under conditions of CFS, compared to the conditions when these stimuli (i.e. a CFS mask and a target stimulus) were presented to one eye (such that they appeared superimposed) instead of using dichoptic presentation (Figure 1.7). Yamashiro et al. (2014) also showed that fMRI activity in V3 and V4 predicted individuals' suppression durations during CFS.

1.4 Why do we need to study binocular rivalry and inter-ocular suppression?

When viewed binocularly, superimposed contours differing in orientation (e.g. orthogonal gratings) are perceived as a plaid. By contrast, rivalry

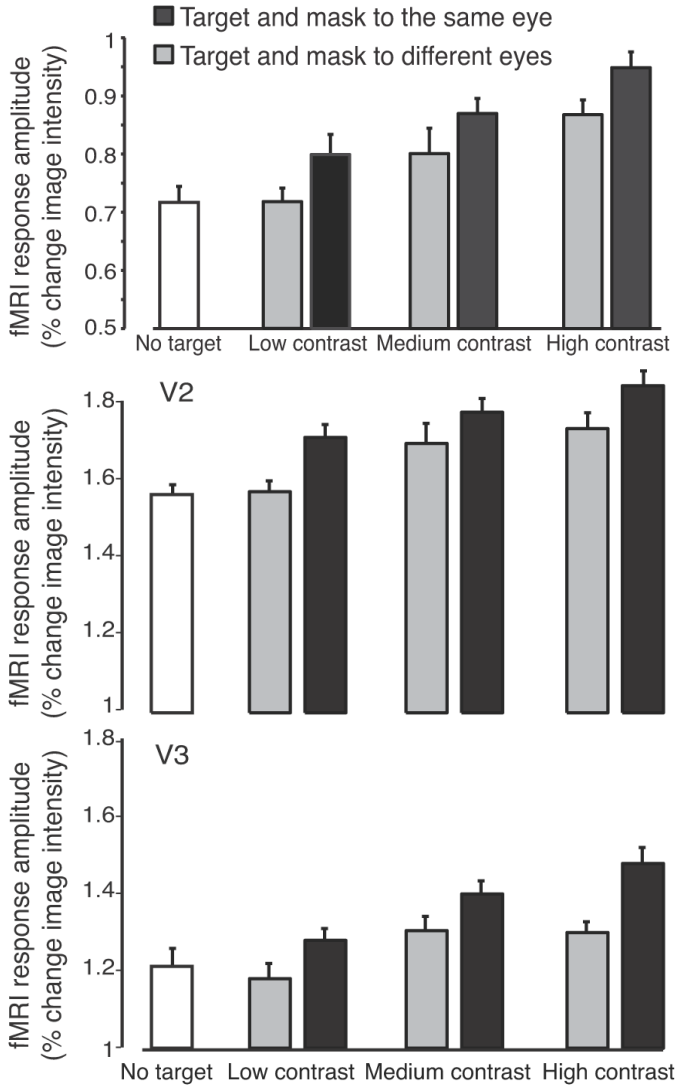


Figure 1.7: Neural correlates of CFS in early visual areas (V1, V2 and V3). fMRI responses increased with the contrast of a target presented to one eye while a CFS stimulus was presented to either the same or different eye. For all contrast levels of the target, the responses were weaker for dichoptic than monocular presentation, indicating inter-ocular suppression produced by CFS. Adapted from Yuval-Greenberg and Heeger (2013).

arises when these are presented dichoptically. Although for the former perceptual alternations between the two are also likely to occur after some period of viewing, the effect is much less robust than that experienced in binocular rivalry (Andrews & Purves, 1997; Campbell, Gilinsky, & Howell, 1973; O'Shea, 1998). This discrepancy places crucial constraints on models of binocular vision, in that a distinction between these perceptual phenomena under different viewing conditions (i.e. binocular/monocular vs. dichoptic) is necessary. For instance, Said and Heeger (2013) proposed an opponency model of binocular rivalry, incorporating neurons that detect inter-ocular conflict, in addition to the competition between orientations taking place within monocular channels (Figure 1.8; also see Katyal et al., 2016; Katyal, Vergeer, He, He, & Engel, 2018). This model has overcome the erroneous prediction of conventional models, that binocularly or monocularly viewed plaid stimuli will result in strong rivalry between the components differing in orientation. Elucidating the mechanisms underpinning inter-ocular suppression and binocular rivalry, therefore, will shed light on how inputs from the two eyes are combined and compete with each other.

Inter-ocular suppression also has relevance to both typical binocular vision, under normal everyday viewing conditions (e.g. images far away from the fixation plane; Arnold, 2011; Arnold, Grove, & Wallis, 2007; O'Shea, 2011), and that associated with abnormal development (e.g. strabismus and amblyopia; Barrett, Bradley, & McGraw, 2004). In both cases, suppression of one eye's image is thought to play a role in minimising perceptual ambiguity and maintaining relatively stable, unified, single vision.

Additionally, there is also practical significance of understanding the mechanisms responsible for inter-ocular suppression. Numerous studies have employed BR or CFS to render a stimulus invisible in order to un-

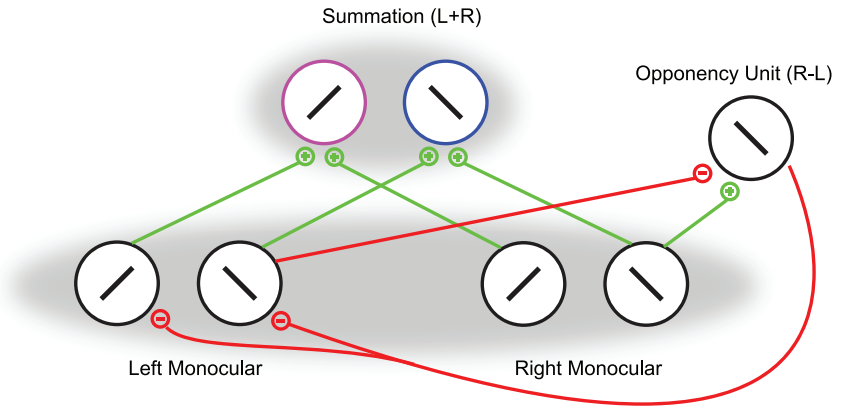


Figure 1.8: Opponency model of binocular rivalry. It is proposed that there is a set of opponency units (with orientation preferences) for each eye that is sensitive to inter-ocular difference. The example shown in this diagram is an opponency unit for the right eye with an orientation preference of –45 degree. Such a unit is activated by the presence of its preferred orientation in the ipsilateral eye (i.e. right eye), but is inhibited by the same orientation in the other eye. The activity of this unit then inhibits all orientations in the contralateral eye through feedback. Activation is indicated by green lines and inhibition is indicated by red lines. Adapted from Said and Heeger (2013).

cover potential visual processing in the absence of awareness (e.g. Adams, Gray, Garner, & Graf, 2010; Bahrami, Carmel, Walsh, Rees, & Lavie, 2008a, 2008b; Cave, Blake, & McNamara, 1998; Costello, Jiang, Baartman, McGlennen, & He, 2009; Heyman & Moors, 2014; Jiang, Costello, & He, 2007; Kaunitz, Fracasso, & Melcher, 2011; Kawabe & Yamada, 2009; Koivisto & Grassini, 2018; Maruya, Watanabe, & Wanatabe, 2008; Moradi, Koch, & Shimojo, 2005; Pasley, Mayes, & Schultz, 2004; Stein & Sterzer, 2012; E. Yang, Hong, & Blake, 2010; Zimba & Blake, 1983). The validity of such an approach, however, may be questionable without a good grasp of the nature of these phenomena.

1.5 Quantifying suppression

To understand the nature of suppression in BR and CFS, it is necessary to measure the amount of suppression for each case. In general, there are two types of measure that researchers commonly use. First, it can be assessed in the temporal dimension—the duration that a given stimulus is suppressed for in the presence of the other stimulus (e.g. Fahle, 1982; Shui'er Han, Blake, & Alais, 2018; Shui'er Han, Lunghi, & Alais, 2016). For example, a breaking-CFS (b-CFS) paradigm is commonly employed to measure the suppression duration; that is, the time taken to detect a test probe (with relatively high or gradually increasing contrast) being suppressed (Jiang et al., 2007; Stein, Hebart, & Sterzer, 2011). Similarly, the predominance of a stimulus (i.e. the proportion of time it dominates perception) is also frequently used to infer the suppression strength of the other stimulus (e.g. Fahle, 1982). Another related measure is the rate of perceptual alternations, whereby slower switches between the two rivalrous percepts are thought to indicate stronger suppression (van Loon et al., 2013; H. R. Wilson, 2007), because it is associated with longer dominance durations. In addition to the measures based on the length of dominance or suppression periods, some rely on the probability of mixed perception, which presumably reflects incompleteness of suppression (e.g. Klink et al., 2010).

Careful considerations should be made, however, when using dynamic and subjective measures to gauge suppression. These types of metrics rely on the estimation over a period of rivalry perception where both rivalrous stimuli are suppressed in turn. Mean dominance duration, or predominance of one stimulus, reveals the degree of suppression of the other stimulus. In this sense, it cannot be used to infer the overall suppression involved in

a given course of rivalry, where the suppression of this stimulus (of which the mean dominance duration/predominance is measured) also occurs[2]. Alternation rate or mixed perception, on the other hand, is determined by suppression of both stimuli. It tells us about the overall level of suppression, but may be less useful to consider the suppression of either stimulus.

Crucially, measures of temporal dynamics cannot reveal the precise depth of suppression, that is, how much sensitivity is reduced. After all it is possible that the suppression associated with different epochs could differ in depth (i.e. detectability of a target), even when the phenomenological perceptual appearance is identical in each case (Alais, Cass, O'Shea, & Blake, 2010; Gayet & Stein, 2017; Kaunitz, Fracasso, Skujevskis, & Melcher, 2014). Moreover, metrics of temporal dynamics do not reflect the susceptibility of a single eye to suppression. The mean duration of a stimulus depends on its ability both to dominate perception and to survive the suppression by the other stimulus. That is to say, they are more or less relative measures. Whilst they are still useful to quantify the relative contributions from the two eyes during inter-ocular suppression, it may be difficult to evaluate the level of suppression between conditions or across individuals.

These issues can be resolved with another type of method, that serves to directly measure the sensitivity of an eye while it is being suppressed by a stimulus presented to the other eye. This is often measured with an objective probe detection paradigm (Fox & Check, 1968, 1972; Tsuchiya et al., 2006). Typically the detection sensitivity to a test probe (e.g. contrast increment) superimposed on a target stimulus to be suppressed, is

[2]In other words, strong suppression of one stimulus may coexist with weak suppression of the other stimulus during rivalry, such that an estimation of the overall suppression level can be equivocal. This limitation can be overcome, however, when only one stimulus but not the other is suppressed (i.e. unilateral inter-ocular suppression), as in the case of CFS.

measured in a forced-choice task using established psychophysical methods such as an adaptive staircase procedure. Depth of suppression can then be quantified by comparing the observed sensitivity, under (suppression phases of) CFS or BR, with that measured in the absence of a suppressing stimulus in the other eye or during the dominance phases. By employing this probe paradigm, Tsuchiya et al. (2006) demonstrated that the depth of suppression induced by CFS is at least five times greater than that rendered by BR under equivalent conditions (Figure 1.9).

Using the probe method to quantify the depth of suppression, however, requires careful considerations of the test probe adopted. Evidence suggests that the degree of sensitivity loss is influenced by the similarity between the probe stimulus and the suppressed stimulus that the probe is superimposed on (Alais et al., 2010; Fox & Check, 1972; Norman, Norman, & Bilotta, 2000; Stuit, Cass, Paffen, & Alais, 2009). That is to say, the changes in sensitivity do not always reflect the degree of suppression engaged in the suppressed field. As Stuit et al. (2009) showed that suppression under rivalry is tuned to the spatial properties of the suppressed pattern (Figure 1.10; also see Section 1.6.2), a superimposed test probe with matched pattern is preferable to be used for estimating the suppression depth in the target field.

Another thing to consider is the temporal profile of the test probe. A well established property of binocular rivalry is that perception is very sensitive to transient changes in the suppressed eye, which can lead to perceptual switches (Blake, Westendorf, & Fox, 1990; Grindley & Townsend, 1965; Walker & Powell, 1979). For that reason, the temporal onset and offset of the probe should be temporally smoothed in order to measure the sensitivity without altering suppression. Moreover, depth of suppression is

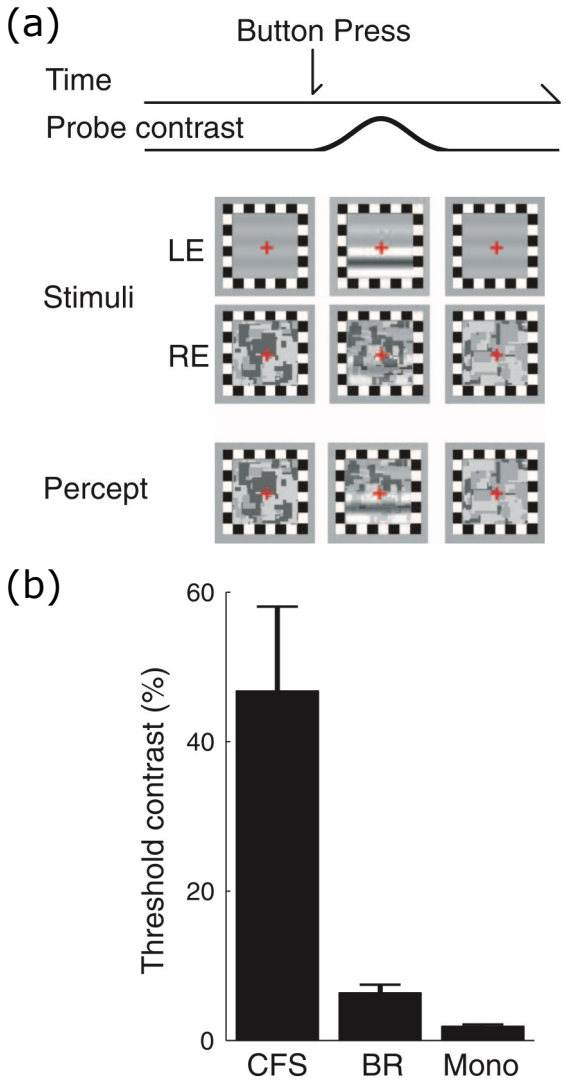


Figure 1.9: An example probe paradigm used by Tsuchiya et al. (2006) to quantify depth of inter-ocular suppression. (a) A suppressing stimulus is presented to the right eye while a target stimulus (grating) is presented to the left eye. A test probe in the form of contrast increment is applied to either the top or bottom half of the target stimulus (bottom in this example), and the threshold to detect this probe is measured. (b) The results showed that the probe threshold was elevated under both conditions of CFS (dynamic suppressing stimulus) and BR (static suppressing stimulus) compared to that measured in the absence of a suppressing stimulus in the other eye (monocular), and such elevation in threshold is used to indicate the depth of suppression. Adapted from Tsuchiya et al. (2006).

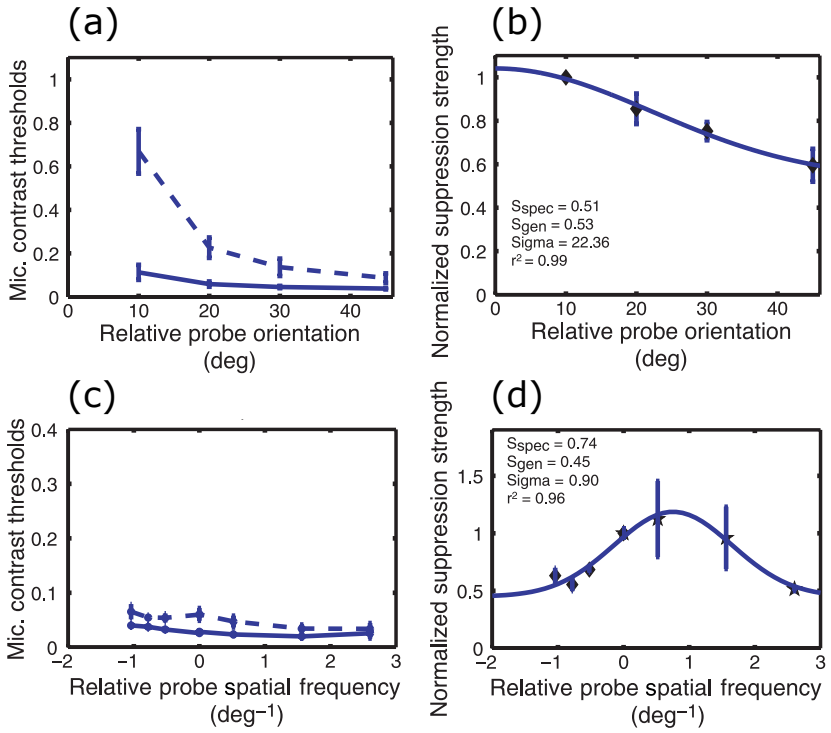


Figure 1.10: Depth of suppression during binocular rivalry is tuned to orientation and spatial frequency. Contrast discrimination threshold was measured during either dominance or suppression phases of binocular rivalry between orthogonally-oriented gratings. The orientation of a test probe was to be judged while its orientation (a–b) or spatial frequency (c–d) was varied relative to that of the pedestal grating the probe was superimposed on. The probe threshold varied as a function of the difference from the pedestal with respect to orientation (a) or spatial frequency (c), when the pedestal was dominant (solid curve) or suppressed (dashed curve). Depth of suppression was estimated by normalising the probe threshold during the suppression state to that during the dominance state, and was found to decrease as the relative orientation (b) or spatial frequency (d) was increased. Adapted from Stuit et al. (2009).

influenced by the relative timing between the presentation of the probe and the suppressing stimulus (see Section 1.9; Kaunitz et al., 2014; Ooi & Loop, 1994; Tsuchiya et al., 2006; Wolfe, 1984). Thus this aspect should also be taken into account when using the probe method to quantify suppression.

In summary, it seems reasonable to conclude that although these two types of measure (temporal dynamics and sensitivity) both signify the effectiveness of suppression, they are not necessarily related. A useful way of distinguishing them is to consider the depth of suppression as the height of a"suppression pulse", and the suppression duration as the width (Fox & Check, 1972). Indeed, an early study by Fox and Check (1972) offered evidence for some degree of independence between how much sensitivity is reduced and how long the stimulus has been suppressed, albeit only three subjects were tested. In addition, whilst inter-ocular luminance and luminance contrast both modulate relative perceptual dominance during BR (Fahle, 1982), they appeared to have little influence on suppression depth (see Section 1.6.2; Holopigian, 1989). Therefore, if the purpose is to compare the suppression under different conditions, it is necessary to ensure the consistency of the measures used for making inferences from the results.

1.6 Is continuous flash suppression a stronger version of binocular rivalry?

While both CFS and BR are characterised by perceptual suppression of one eye's image along with simultaneous visibility of an image presented to the other eye, they are not necessarily mediated by the same underlying mechanisms. A prominent distinction between these two phenomena is the robust, reliable, unilateral suppression that is rendered by CFS, whereas in

BR perception switches back and forth between the suppression of either image. However, one might argue that they are not fundamentally different—the short-lived bistable phases of dominance and suppression during BR are merely a matter of weakness such that sustained suppression of one eye cannot be maintained. This section will address this issue by reviewing the existing evidence in the literature.

1.6.1 Revisiting Levelt's second proposition of binocular rivalry

A distinct property of BR proposed by W. J. M. Levelt (1965) in his monograph *On binocular rivalry* is the second proposition—increasing the physical strength of one stimulus only reduces the mean dominance duration of the other stimulus, leaving that for the former minimally affected. Levelt used the term *stimulus strength*, to describe the ability of a stimulus to dominate perception during the course of binocular rivalry (which is roughly equivalent to stimulus predominance). He included density, luminance contrast and blur as parameters of stimulus strength, but a number of other stimulus attributes such as colour contrast (Bossink, Stalmeier, & de Weert, 1993) are also considered nowadays.

The second proposition has been commonly regarded as a defining characteristic of BR. Upon the first introduction of CFS, Tsuchiya and Koch (2005) argued for a distinction from BR, based on the fact that their data violated the aforementioned proposition. Specifically, the manipulation of the suppressing stimulus strength, by varying the refresh rate of the dynamic stimulus[3], mainly affected the phase duration of this varying stimulus other

[3]Tsuchiya and Koch (2005) treated the flash rate as a parameter of stimulus strength because it modulates stimulus predominance as shown by their findings (see Figure 1.11a).

than the one that had fixed strength (Figure 1.11).

Nevertheless, it has been over five decades since Levelt's propositions were put forward, and a number of modifications have subsequently been developed to the original concepts (for a review, see Brascamp, Klink, & Levelt, 2015). Whereas many empirical findings can still be captured by this proposition (Blake, 1977; Fox & Rasche, 1969; Leopold & Logothetis, 1996; W. J. M. Levelt, 1966b; Logothetis, Leopold, & Sheinberg, 1996), others have also reported altered dominance duration of the varying stimulus, albeit modestly (Bossink et al., 1993; Mueller & Blake, 1989). A limitation of these studies is that they all manipulated the strength of the weaker stimulus while keeping that for the stronger one constant—the strength of the fixed stimulus was invariably higher than the other varying stimulus. Indeed, when the strength of the stronger stimulus was varied in several more recent studies, findings that appear to violate W. J. M. Levelt's (1965) second proposition were in fact obtained. For instance, in Brascamp, van Ee, Noest, Jacobs, and van den Berg's (2006) study the contrasts of both stimuli were manipulated in a factorial manner. Increasing the contrast of a stimulus largely increased its own dominance duration when the other stimulus had a lower contrast (Figure 1.12). A modified version of this proposition now seems more suitable to describe the dependence of dominance duration on stimulus strength. That is, increasing the strength of a stimulus primarily influences the mean dominance duration of whichever has the greater strength of the two (Brascamp et al., 2015). This is visualised in Figure 1.13.

It may be possible to reconcile Tsuchiya and Koch's (2005) observations of CFS with this modified version of Levelt's second proposition of BR. The dynamic suppressing stimulus tested had higher effective strength than the

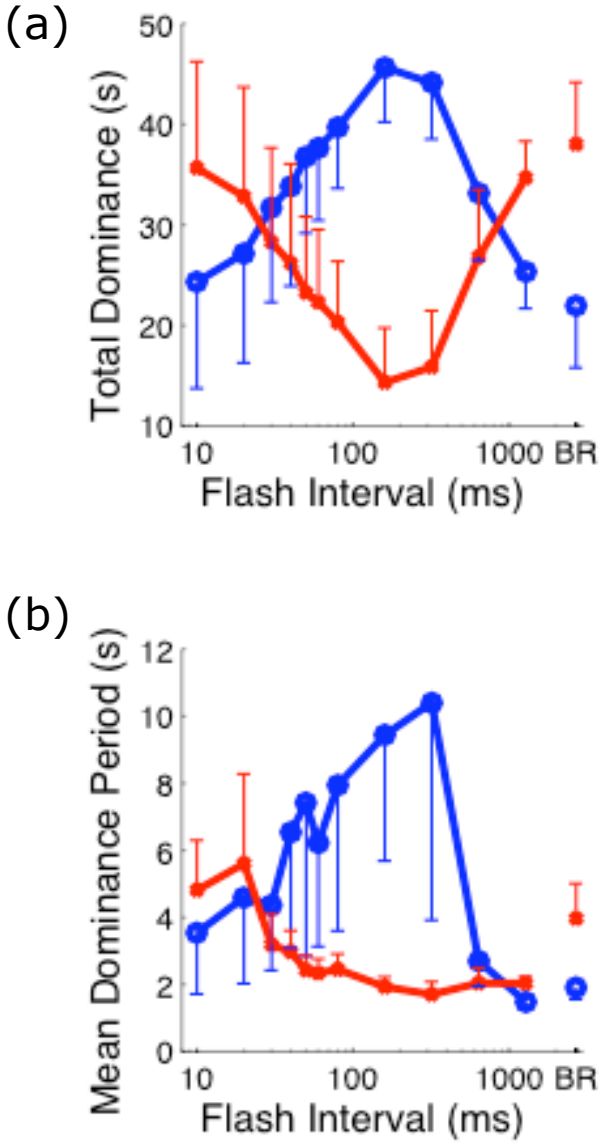


Figure 1.11: The modulation of stimulus predominance (a) and mean dominance duration (b) of the CFS flashing stimulus (blue) and the target stimulus (red) by flash interval. As flash rate modulates stimulus predominance, it can be regarded as a type of stimulus strength. That varying the flash rate of the CFS stimulus primarily affected the mean dominance duration of this stimulus violated W. J. M. Levelt's (1965) second proposition of binocular rivalry. Adapted from Tsuchiya and Koch (2005).

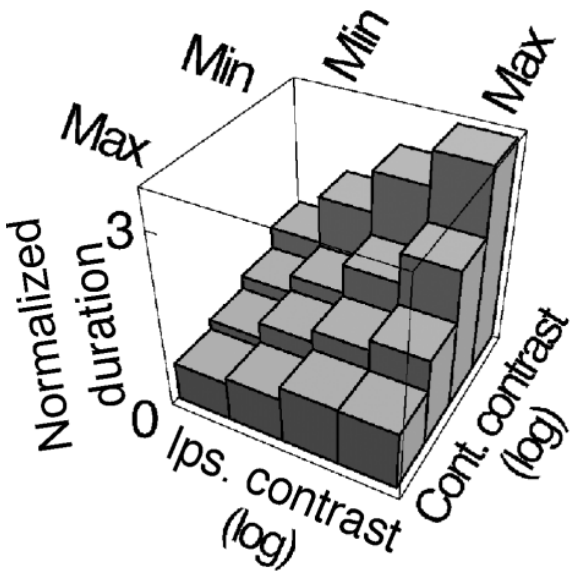


Figure 1.12: Mean (normalised) dominance duration varied as a function of ipsilateral and contralateral contrast during binocular rivalry. Adapted from Brascamp et al. (2006).

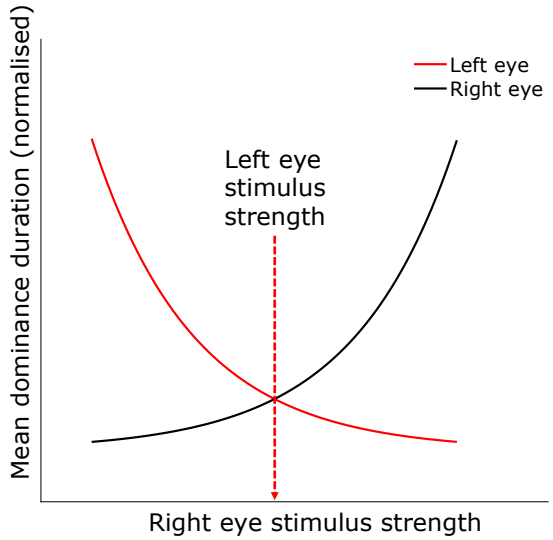


Figure 1.13: An illustration of a modified Levelt's second proposition. Increasing the strength of the right eye stimulus (abscissa), affects rivalry dynamics primarily by decreasing the mean dominance duration of the left eye stimulus (whose strength is marked by the red dashed line) when the strength of the latter is greater (to the left of the dashed line), and by increasing the duration of the right eye stimulus itself when it has the greater strength (to the right of the dashed line). Note that these curves are only for the purpose of illustrating the directions of the effects, but they have no real values. Figure recreated from Brascamp et al. (2015).

stationary stimulus (indicated by the greater predominance of the former), justifying the dependence of dominance duration of the dynamic stimulus on its own strength.

1.6.2 Stimulus selectivity

One way to determine whether the difference between BR and CFS is merely quantitative is to look at their dependence on stimulus properties. If they are governed by the same neural process, they should elicit comparable patterns of behaviour as a function of the stimulus parameters. Whilst a great deal of work has examined this issue, it remains indeterminate in part because of confusion about the use of the phrase "stimulus selectivity". It can sometimes mean the dependence of suppression on the attributes of the stimuli that induce rivalry or suppression, and other times it is with respect to the features being suppressed (i.e. whether some features are more suppressed than others). It is therefore necessary to make it clear what stimulus selectivity refers to when addressing this issue.

How does suppression depend on the features of inducing stimuli?

As noted by Wheatstone (1838) and also indicated in Levelt's propositions of BR, stimulus predominance can be modulated by the physical properties of each eye's image, regardless of the unpredictability of individual phases. Thereafter, numerous studies have examined the dependence of rivalry suppression on a number of different stimulus parameters. The results show that the effectiveness of suppression of a stimulus (inferred from various dynamic measures[4]; see Section 1.5) increases with the differences between the

[4]As during BR the two stimuli are suppressed in turn, the suppression duration of one stimulus is a relative measure that is only meaningful given that of the other rivalrous stimulus. Not to be confused with the overall level of suppression involved, or the

dominant and the suppressed stimuli in terms of luminance (Fahle, 1982; Kakizaki, 1960), luminance contrast (Bossink et al., 1993; Brascamp et al., 2006; Fahle, 1982; Katyal et al., 2016; Leopold & Logothetis, 1999; Mamassian & Goutcher, 2005; Meng & Tong, 2004; Platonov & Goossens, 2013; Song & Yao, 2009; Whittle, 1965), colour contrast (Bossink et al., 1993), and motion velocity (Blake et al., 1998; Blake, Zimba, & Williams, 1985; Bossink et al., 1993; N. J. Wade, de Weert, & Swanston, 1984). Take luminance contrast as an example, Song and Yao (2009) have demonstrated that increasing the inter-ocular imbalance in contrast increased the probability of dominance at rivalry onset for the stimulus with the higher contrast of the two, and also increased its mean dominance duration relative to that of the other stimulus (Figure 1.14). Notably, the attributes stated above can all be regarded as examples of stimulus strength, in the sense that a value on each scale can be classified as weaker or stronger. On the other hand, for the stimulus attributes that are not explicitly decoded in such a monotonically scalar manner, such as orientation (Andrews & Purves, 1997; D. H. Baker & Graf, 2009b; O'Shea, 1998), spatial frequency (O'Shea, 1998; Y. Yang et al., 1992; but see N. J. Wade et al., 1984), and hue (Andrews & Purves, 1997), the level of suppression during BR seems to decrease with increasing inter-ocular difference in these dimensions. For example, perceptual alternations became more frequent, implying reduced overall suppression, as the two stimuli were more disparate in orientation or hue (Figure 1.15; Andrews & Purves, 1997). Curiously, contradicting findings have also been obtained—that is, the depth of suppression elicited by BR is independent of the luminance, luminance contrast, or spatial frequency of the inducing stimuli (Holopigian, 1989). It should be noted, however, that these results

suppression of the other stimulus, which does not necessarily scale positively with the suppression of this stimulus.

were measured by a reduction in detection sensitivity, whereas the findings suggestive of stimulus selectivity of BR were based on temporal dynamics. As discussed in Section 1.5, these two types of measures do not necessarily reflect the same aspects of suppression, which may explain the discrepancies in the results. It is therefore important to bear this distinction in mind when making inferences based on these findings.

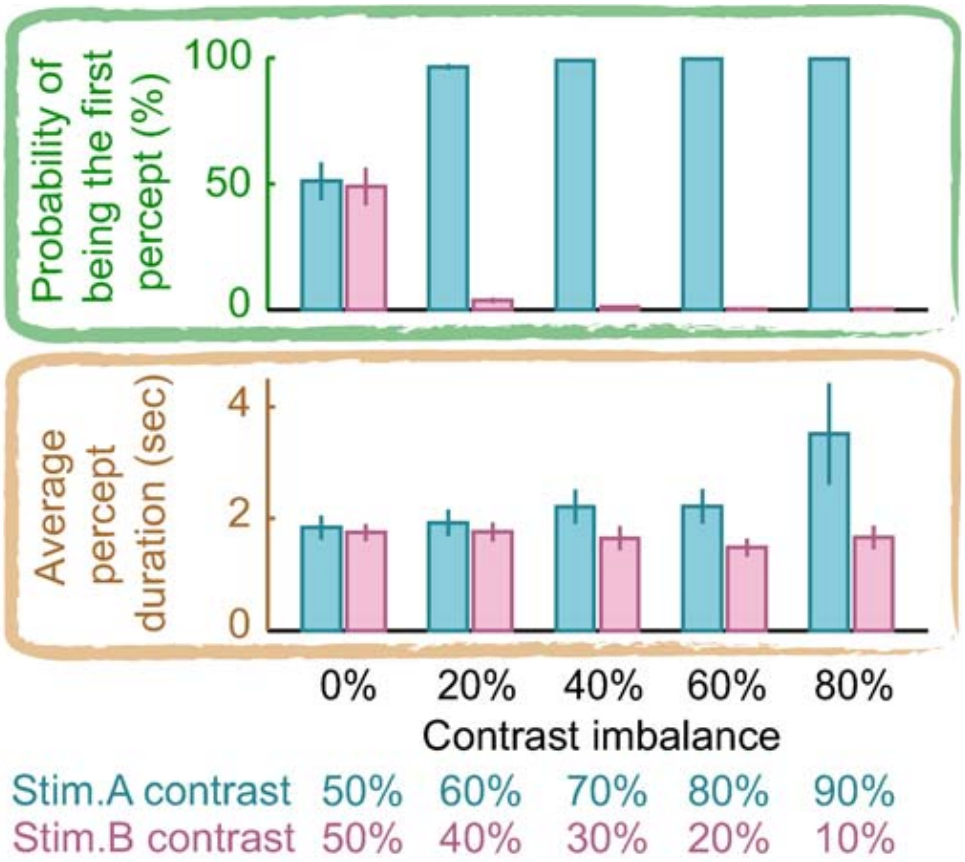


Figure 1.14: The dependence of relative dominance during binocular rivalry on inter-ocular imbalance in luminance contrast. The stimulus having the higher contrast of the two became more likely to be dominant at the onset of rivalry (top panel) and also dominated perception for longer periods on average (bottom panel), as the difference in contrast between the two eyes' stimuli was increased. Adapted from Song and Yao (2009).

As discussed in Section 1.6.1, the dependence of mean dominance duration of the flashing stimulus on flash rate under CFS is compatible with

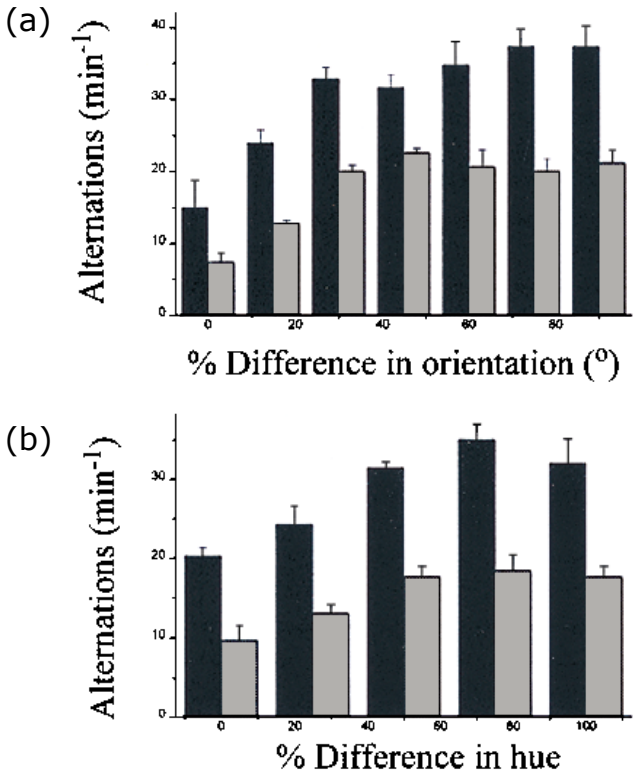


Figure 1.15: Alternation rate of binocular rivalry increased (indicating reduced level of suppression) when the difference in orientation (a) or hue (b) between the two eyes' stimuli was increased. Black and grey bars are data for two individual observers. Adapted from Andrews and Purves (1997).

a critical property of BR, implying the possibility of similar temporal dynamics. Specifically, Tsuchiya and Koch (2005) showed that increasing the refresh rate of the dynamic Mondrian pattern up to 10 Hz lengthened its dominance duration. The duration then decreased when this suppressing stimulus flashed at a higher rate, in synchrony with the decline in its predominance, or stimulus strength (see Figure 1.11, blue lines).

When looking at the dependence of suppression (measured with temporal dynamics or reduction in sensitivity) under CFS on inter-ocular feature differences, similar results to BR were obtained with respect to luminance (Ledgeway, McGraw, & Thompson, 2013) and luminance contrast (Shui'Er Han, Lukaszewski, & Alais, 2019; Shui'er Han et al., 2016; Kaunitz et al., 2014; Ledgeway et al., 2013; Yuval-Greenberg & Heeger, 2013). The higher the luminance or contrast of the suppressing stimulus relative to the target, the longer the suppression of the latter, which is again in line with the notion of stimulus strength.

As for stimulus attributes that do not straightforwardly operate as a dimension of stimulus strength, the differences between the two eyes' images seem to impair suppression evoked by CFS, similar to the situations under BR. Specifically, suppression has been found to be largest when the features of the flashing stimulus match those of the to-be-suppressed stimulus, with respect to orientation (T. Y. Gao et al., 2016, 2018; Shui'Er Han & Alais, 2018), spatial frequency (E. Yang & Blake, 2012), and more generally, spatial patterns (Shui'er Han et al., 2018). For example, T. Y. Gao et al. (2018) have demonstrated orientation tuning of suppression evoked by CFS, in which the depth of suppression of a target declined as the orientation difference from the dynamic noise was increased from 0 to 90 degrees (Figure 1.16). In addition, a low spatial-frequency target was found to be

suppressed to a greater extent than a target having a higher frequency, by a CFS stimulus that contained predominantly low spatial-frequency energy (Figure 1.17; E. Yang & Blake, 2012). Such a low-frequency bias of suppression was however diminished, and even eliminated, when the CFS stimulus was filtered to contain only high spatial frequencies. These observations also imply that the matching between the two eyes' stimuli in dimensions that may not monotonically scale with stimulus strength promotes strong suppression under CFS.

Although the evidence mentioned above suggests similarities between the dependence of suppression elicited by BR and CFS on stimulus features, the observations regarding the role of temporal rate seem more complicated to interpret. The original form of CFS described by Tsuchiya and Koch (2005) was induced by a dynamic mask and a static target. If the temporally transient components contained in the mask serve to increase stimulus strength, as would be predicted by the superiority of CFS over BR in producing suppression (perhaps by minimising neural adaptation of the mask, see Section 1.7), one would expect monotonically increasing suppression as the mask refresh rate is increased. Some studies have indeed adopted this assumption and used a very high mask rate in order to maximise suppression (e.g. S. Xu, Zhang, & Geng, 2011). Yet, as already mentioned, this is not the pattern of the results found—suppression peaks at a certain update rate of the mask[5] (see Figure 1.11; but see Kaunitz et al., 2014). The decline in effectiveness in exerting suppression at higher mask flicker rates, however, may be explained by the temporal acuity limit of the human visual system. That is, at the highest update rates, much of the mask stim-

[5]There is however some variation in what is reported to be the optimal rate that triggers the strongest suppression effect (Shui'er Han et al., 2018; Shui'er Han et al., 2016; Kaunitz et al., 2014; Zhan, Engelen, & de Gelder, 2019; Zhu, Drewes, & Melcher, 2016).

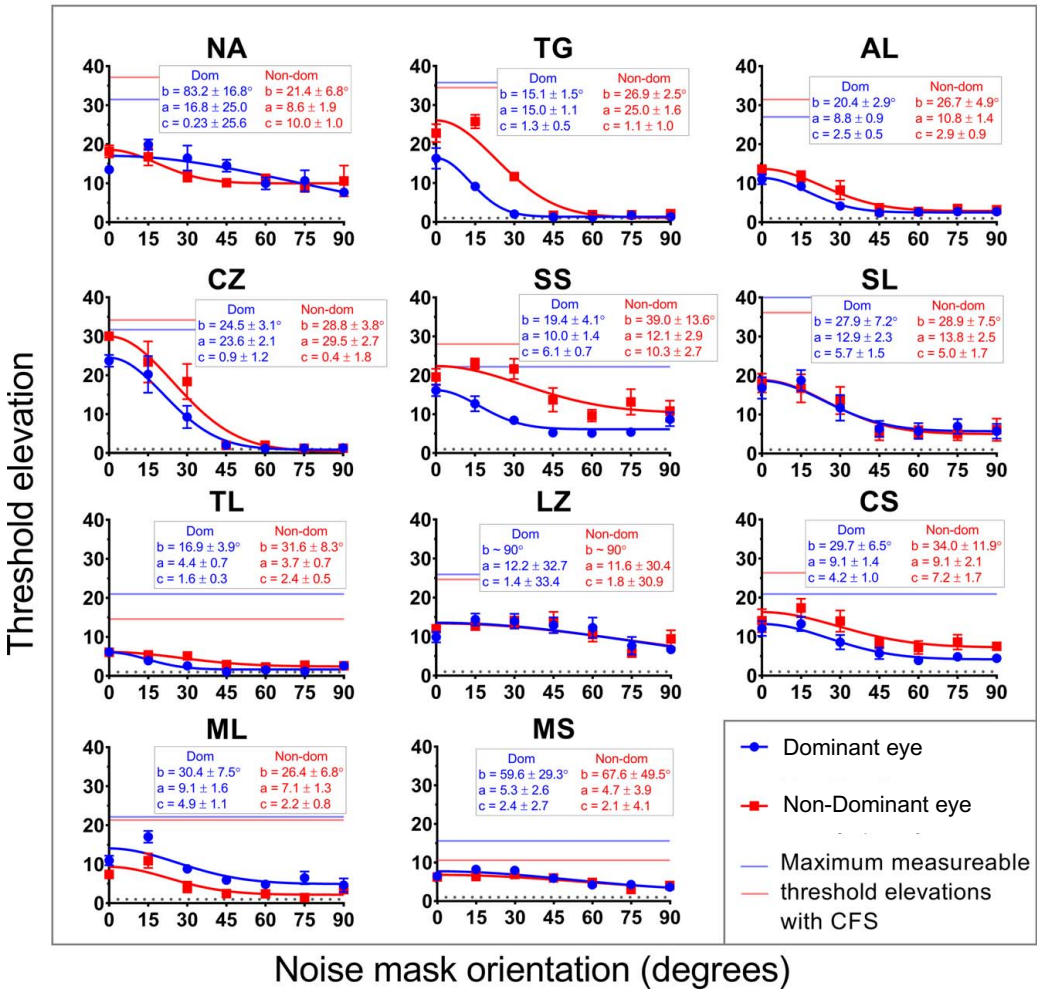


Figure 1.16: Threshold elevation under CFS as a function of orientation difference between the dynamic noise and the target grating for the dominant eye and the non-dominant eye in a group of participants with normal binocular vision. For most of the observers, the depth of suppression was maximum when the orientations of the two stimuli were the same (i.e. 0 degree noise mask), and declined as the difference was increased. Adapted from T. Y. Gao et al. (2018).

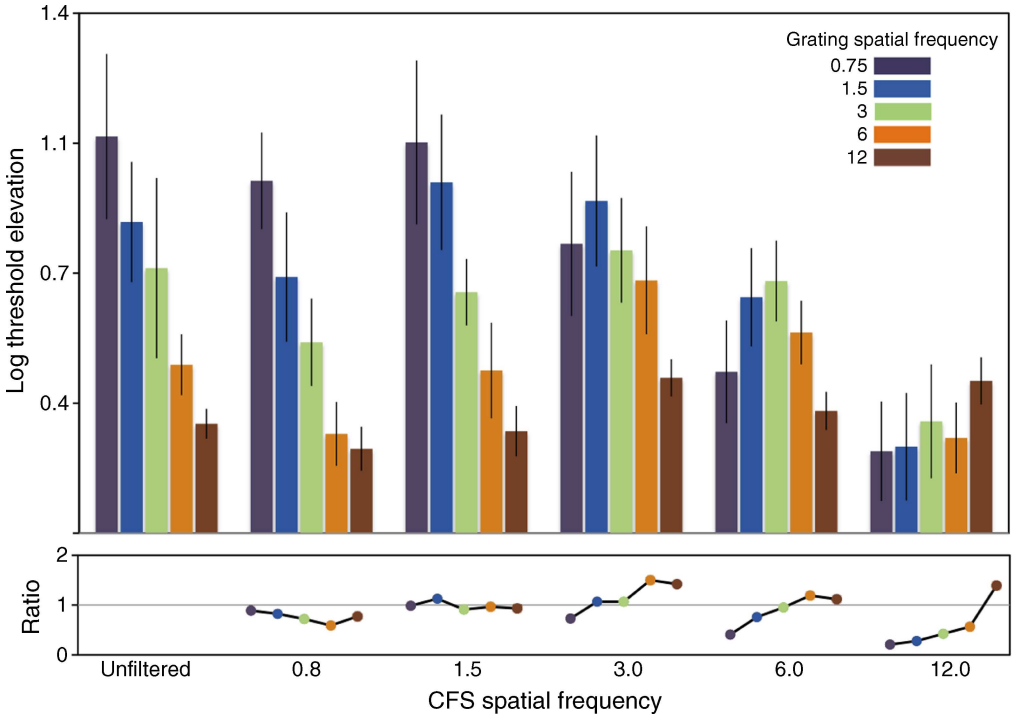


Figure 1.17: The dependence of threshold elevation on spatial frequencies of the CFS suppressing stimulus and the target. The CFS stimulus (dynamic Mondrians) was either spatially broadband (unfiltered), or band-pass filtered with a centre frequency indicated by the abscissa. The coloured bars show the data for different spatial frequencies of the target. With an unfiltered CFS stimulus (that had a low-biased spatial-frequency power spectrum), the elevation in threshold to detect a target decreased with the target frequency was increased. With a filtered CFS stimulus, such an effect was only true when the centre frequency was low but became increasingly invalid as the CFS stimulus contained higher frequencies. The bottom plot shows the ratio of threshold elevation produced by a filtered CFS stimulus with a given centre frequency to that produced by an unfiltered CFS stimulus for the corresponding target frequency. Adapted from E. Yang and Blake (2012).

ulus' contrast energy is effectively outside the temporal window of visibility (Elliott, Whitaker, & MacVeigh, 1990; Movshon, Thompson, & Tolhurst, 1978; Robson, 1966; Tolhurst & Movshon, 1975; Virsu, Rovamo, Laurinen, & Näsänen, 1982). Therefore, this is not inconsistent with the idea that transient energy is a form of stimulus strength. This is also compatible with the findings in BR showing dependence of suppression on motion velocity (Blake et al., 1998; Blake et al., 1985; Bossink et al., 1993; N. J. Wade et al., 1984). These studies found that a moving stimulus was more dominant than a stationary competing stimulus. When two moving stimuli were rivalling, the faster stimulus predominated over the stimulus that moved at a slower speed, and such a difference in predominance decreased as the speed difference between the two stimuli was decreased (Figure 1.18; Blake et al., 1998). However, this was only true when the speed of the faster stimulus did not exceed a certain value, and the predominance of that stimulus started to decrease when its speed was further increased. This pattern of results was very similar to what was found with CFS when flash rate was varied (cf. Figure 1.11a).

Interestingly, Moors, Wagemans, and De-Wit (2014) revealed strongest CFS suppression when the temporal rates of the mask and the target were matched. This pattern of modulation is however more similar to non-stimulus-strength parameters[6] such as orientation. Furthermore, some studies have shown that a mask stimulus with low temporal frequencies is more effective at suppressing a static target than a mask containing higher frequencies (Shui'er Han et al., 2018; Shui'er Han et al., 2016; E. Yang & Blake, 2012). It seems difficult to reconcile these mixed patterns of results on the role of temporal energy with the current understanding of CFS, and

[6]Those do not monotonically scale with stimulus predominance.

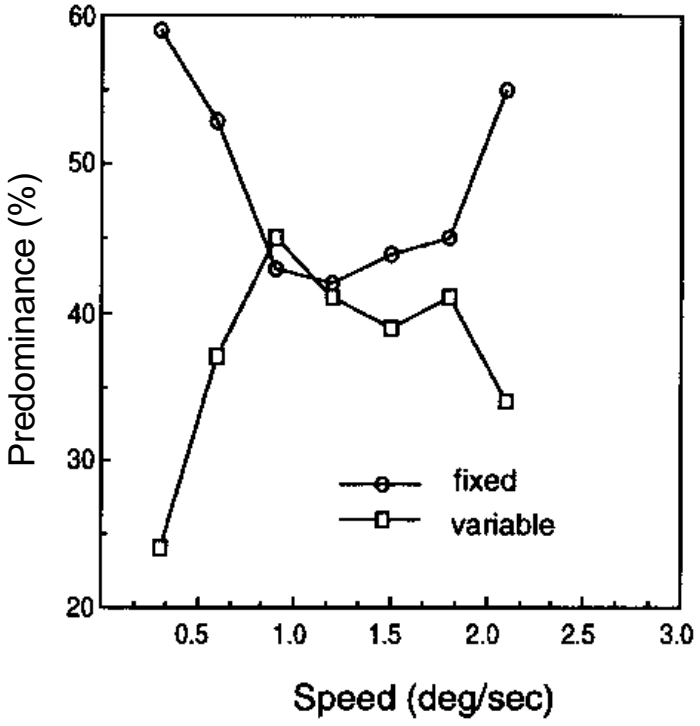


Figure 1.18: Stimulus predominance during binocular rivalry between two moving stimuli. One of the stimuli moved at a fixed speed (1.2°/s), while the speed of the other stimulus was varied and was indicated by the abscissa. Adapted from Blake et al. (1998).

further research is therefore necessary to disentangle this problem.

What is suppressed during BR and CFS?

Although some early work pointed to a feature non-selective view of BR (Fox & Check, 1966; Wales & Fox, 1970), in that all features (in a suppressed field) are invariantly suppressed, this has been subsequently challenged by many later studies. For example, it has been demonstrated that luminance and colour perception are differentially affected under BR suppression and that suppression is selective to wavelength (Figure 1.19; Ooi & Loop, 1994; Smith III, Levi, Harwerth, & White, 1982; Smith III, Levi, Manny, Harwerth, & White, 1985). Moreover, Stuit et al. (2009) showed that BR suppression is tuned to the specific features (i.e. orientation and spatial frequency) of the suppressed stimulus (see Figure 1.10) but only in terms of the dimension of conflict between the two eyes that triggers rivalry in the first place. In a similar vein, selective reduction in sensitivity was found for motion and form information, depending on whether it was motion or form rivalry (Figure 1.20; Alais & Parker, 2006). Comparable results have also been revealed with CFS. It has been shown that identification of colour and form are dissociable under the suppression evoked by CFS (Figure 1.21; Hong & Blake, 2009) and that temporal information is less suppressed than spatial information (Zadbood, Lee, & Blake, 2011). These findings led to a feature-selectivity explanation for both suppression evoked by BR and by CFS. Therefore, it seems reasonable to reject the belief that inter-ocular suppression purely relies on mutual competition between the eyes (e.g. Blake, Westendorf, & Overton, 1980).

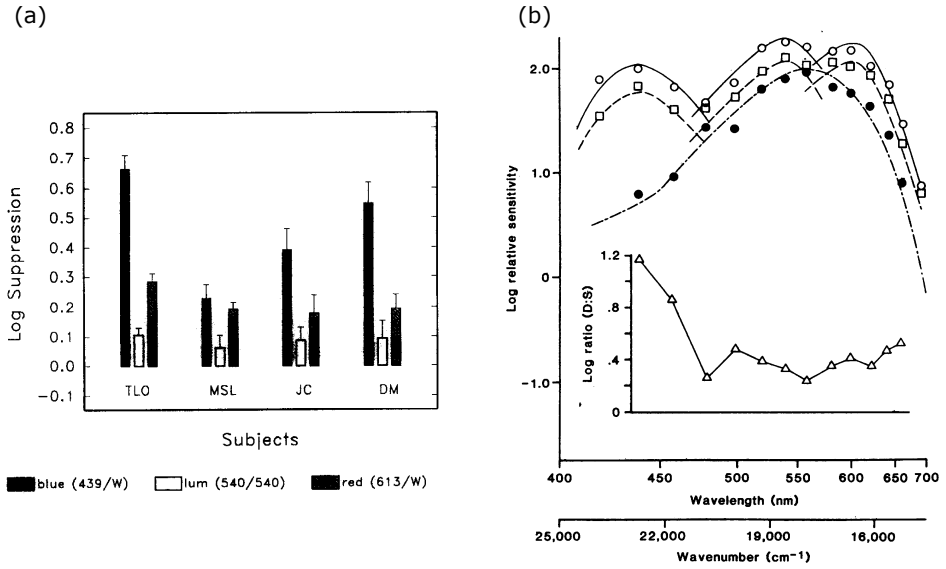


Figure 1.19: Wavelength dependence of binocular rivalry suppression. (a) Depth of suppression (for four individual observers) was indicated by the elevation in threshold during suppression compared to that during dominance, for detecting an isoluminant change in colour (either short or long wavelength) against a white background, or a change in intensity (luminance). These data revealed that BR suppression impaired colour sensitivity more than luminance sensitivity and that within the colour system short wavelengths were suppressed more severely than long wavelengths. Adapted from Ooi and Loop (1994). (b) Colour sensitivity during dominance (open circles) and suppression phases (filled circles) as a function of wavelength. The data measured under binocular viewing (nonrivalrous) are also shown (open squares). The log ratio of the sensitivities during dominance to suppression phases is plotted in the inset. Depth of suppression was highest for short wavelengths, resulting from distinct patterns of dependence on wavelength for dominance (three peaks) and suppression (a single peak). Adapted from Smith III et al. (1982).

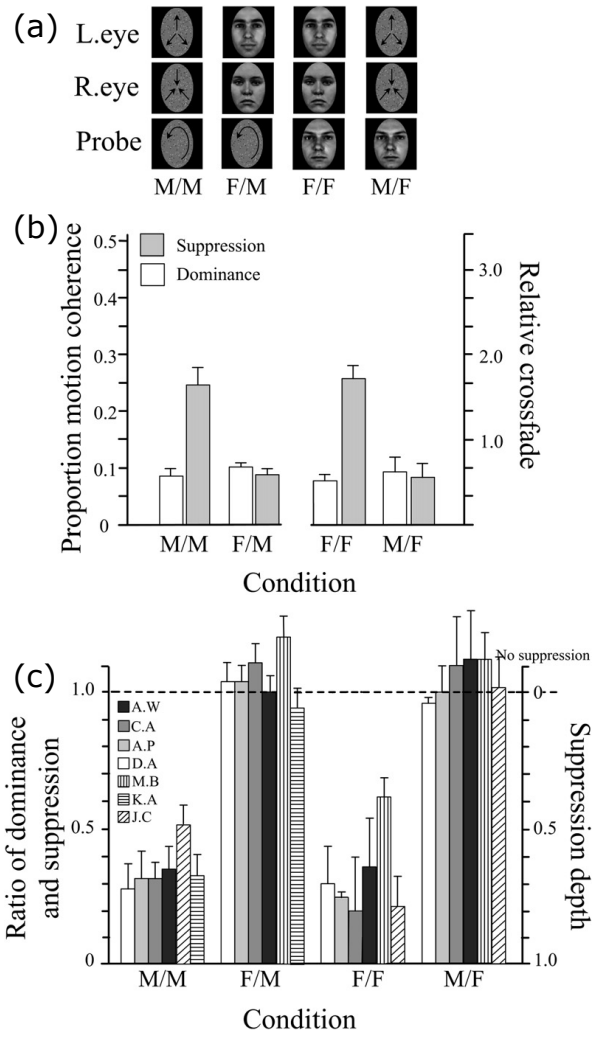


Figure 1.20: Selective suppression of motion and face information during binocular rivalry between motion or face stimuli. (a) Binocular rivalry was induced by a pair of random dot kinematograms (RDK) undergoing global motion, or face images. The task was to identify the motion direction of a RDK probe or to judge whether a face probe was one of the predesignated faces (known to the observer). (b) Sensitivity during dominance or suppression was measured by either motion coherence threshold for a RDK probe (left panel) or contrast threshold for a face probe (right panel). Note that the latter was computed in the form of relative crossfade which is the ratio of probe contrast at threshold to the contrast of the rivalrous stimuli. (c) The ratio of dominance to suppression calculated from the data shown in (b) but for individual observers. The right ordinate indicates the corresponding depth of suppression. These results suggest that motion rivalry selectively impairs motion sensitivity and face rivalry selectively impairs face sensitivity. Adapted from Alais and Parker (2006).

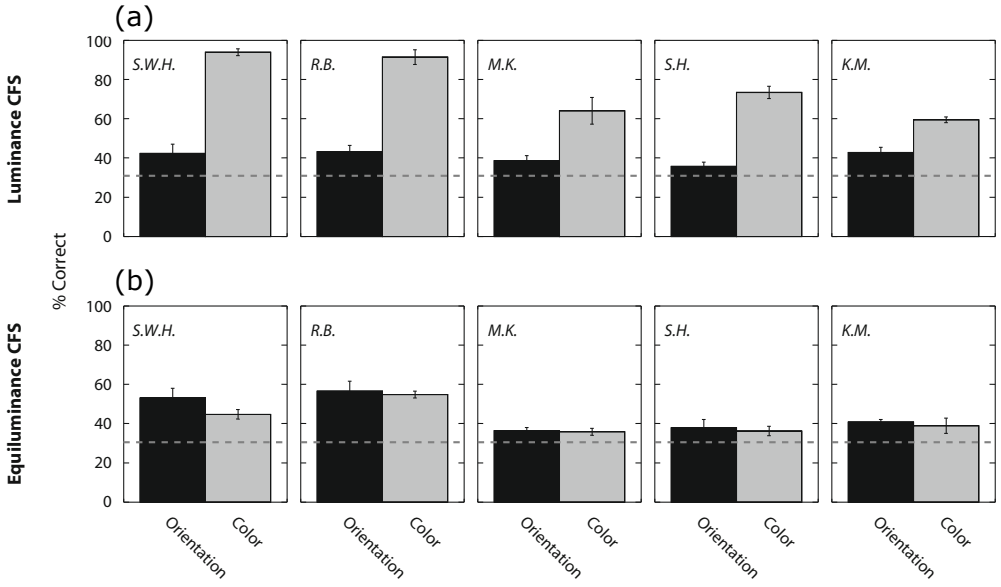


Figure 1.21: Color and form sensitivities were differentially impaired by suppression under CFS. Percentage of correct responses (measured in five observers) for identifying the colour of a target (grey bars) was higher than that for orientation identification (black bars) when it was suppressed by an achromatic CFS stimulus (a), but the two performances were comparable when the target was suppressed by a chromatic CFS stimulus (b). Adapted from Hong and Blake (2009).

Conclusion

As reviewed in this section, both BR and CFS are selective to stimulus features, in terms of the ability to elicit suppression and susceptibility to suppression. In addition to basic features, the level of suppression in each case, can be influenced by higher-level factors of stimulus content such as global context (BR: Alais & Blake, 1998; Alais & Blake, 1999; Fukuda & Blake, 1992; Kovács, Papathomas, Yang, & Fehér, 1996; Ooi & He, 2003; Sobel & Blake, 2002; Stuit, Paffen, van der Smagt, & Verstraten, 2011; Vergeer & van Lier, 2010; CFS: L. Wang, Weng, & He, 2012; but see, Moors, Wagemans, Van Ee, & De-Wit, 2016) and behavioural relevance (BR: Arnold et al., 2007; D. H. Baker & Graf, 2009a; CFS: Jiang et al., 2007). We may conclude that neither BR nor CFS is an all-or-nothing phenomenon, and that they are likely to be mediated by common mechanisms. Nevertheless, it is also important to note the discrepancies between BR and CFS (Holopigian, 1989; Ledgeway et al., 2013). It is possible, albeit speculative, that the transient components contained in the mask used for a CFS task amplifies within-channel inhibition between eyes (e.g. inhibition between orientation channels in each eye that optimally respond to similar orientations) while having much less, or little influence on cross-channel inhibition (e.g. inhibition between orientation channels in each eye that optimally respond to very different orientations). Although further work is needed to corroborate this idea, it has already gained support from the findings that a flashing mask stimulus was no more effective than a static equivalent to elicit cross-channel suppression (Maehara, Huang, & Hess, 2009).

1.6.3 Sequential dependence

Until the last decade, sequential independence was considered to be one of the defining features of BR. That is, the duration of each individual period of dominance or suppression state does not depend on one another (Blake et al., 1971; Fox & Herrmann, 1967; Lehky, 1995; W. J. M. Levelt, 1965; Logothetis et al., 1996; Walker, 1975). This idea has been challenged by the observation that perception during BR is influenced by the observer's recent perceptual history and that phase durations show some degree of serial correlation (J. B. Gao et al., 2006; Mamassian & Goutcher, 2005; Pastukhov & Braun, 2011; Van Ee, 2005; van Ee, 2009). Interestingly, serial correlations have also been reported between suppression durations produced by CFS (Moors, Stein, Wagemans, & van Ee, 2015). The sequential dependence found in both cases is likely to be due to neural adaptation of the mechanisms encoding each eye's image (see Section 1.7), whilst the correlation is disrupted when the presentation of stimuli is swapped between eyes in order to prevent adaptation (Moors et al., 2015; van Ee, 2009). These findings, therefore, have an important bearing on the understanding of the relationship between BR and CFS by suggesting a common process.

1.7 Reciprocal inhibition and adaptation

Over the past few decades, several computational models have been constructed in an attempt to explain binocular rivalry and inter-ocular suppression at the neuronal level. Although many models are based on the validity of Levelt's propositions, which have undergone several modifications (see Section 1.6.1; Brascamp et al., 2015), they still remain useful for our understanding of the underlying inter-ocular interactions.

The most prominent models of BR rely on the notion of reciprocal inhibition between the mechanisms encoding conflicting input from the two eyes and adaptation of these mechanisms over time, in an attempt to account for the occurrence of perceptual alternations (Blake, 1989; Kalarickal & Marshall, 2000; H. R. Wilson, 2003, 2007, 2017). This type of model also has relevance to other non-bistable (i.e. unilateral) forms of inter-ocular suppression, which we will return to later in this section.

In H. R. Wilson's (2007) model, suppression of one eye's stimulus is through inhibition elicited by neurons that are activated by the monocular neurons encoding the conflicting stimulus in the other eye (Figure 1.22); this inhibition then implements the dominance of the latter stimulus. This is based on an early idea by Breese (1899) that neurons encoding different stimulus representations that are mutually exclusive compete with each other and perceptual dominance is determined by the stronger activation (i.e. the "winner"). The excited activity of such inhibitory neurons subsequently undergoes a slow self-adaptation process, presumably by means of hyperpolarisation, that gradually reduces its own activity until it reaches a critical level below which the suppressed unit is released from inhibition and thereby becomes activated. In this way the unit encoding each eye's input gains activation in alternation. This implementation entails phase durations with high sequential correlations which are not characteristic of typical rivalry dynamics, but durations having a gamma distribution can be reproduced by adding random noise to the model[7] (Kang & Blake, 2010; H. R. Wilson, 2007).

[7]Some models propose that noise alone without adaptation is sufficient to produce typical temporal dynamics of BR, presumably by inducing random perturbations in the neuronal activity level associated with each percept (e.g. Moreno-Bote, Rinzel, & Rubin, 2007), but Kang and Blake (2010) revealed a dependence of dominance duration on prior adaptation which is difficult to reconcile with noise.

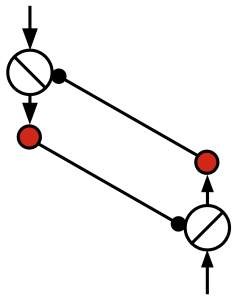


Figure 1.22: An example basic element of reciprocal inhibition. A neuron (shown in red) activated by a monocular neuron encoding the left-tilted orientation in one eye inhibits another monocular neuron encoding the right-titled orientation in the other eye and vice versa. Excitation is indicated by arrowed lines and inhibition is indicated by the lines ending with a dot. Adapted from H. R. Wilson (2017).

The account of mutual inhibition with self-adaptation predicts gradually decreased activity associated with the eye being dominant, following the onset of a single dominance period, accompanied by a declined suppression strength on the other eye. In support, Alais et al. (2010) showed that probe sensitivity waned over the course of a dominance phase, whereas it increased towards the end of a suppression phase (also see Dieter, Melnick, & Tadin, 2015). Similarly, prior visual adaptation for a brief period (comparable to rivalry phase durations) reduces the subsequent duration for which a stimulus dominates perception (Kang & Blake, 2010). Blake, Sobel, and Gilroy (2003) have also demonstrated that alternation rate was slowed under conditions minimising local adaptation. These observations all point to a role of neural adaptation in triggering perceptual switches during competition between two incompatible monocular images.

This idea provides a possible explanation for the sustained suppression produced by CFS—the transient nature of the flashing stimulus might serve to preclude or reduce adaptation of the mechanism encoding this stimulus, such that it can dominate perception for a relatively prolonged period of

time when competing with the mechanism encoding a static image presented to the other eye. However, H. R. Wilson's (2007) simple model does not include such a component that allows for the prevention of the self-adaptation process by the specific properties of the CFS stimulus. This is resolved in an extended model with an added parameter of stimulus feature, and the model simulation is able to reproduce the dependence of CFS suppression on flash rate (Shimaoka & Kaneko, 2011). This model predicts that the more features (e.g. orientation, spatial phase) a CFS stimulus contains over multiple flashes, the stronger the suppression it evokes. This is because when one feature is off at a given flash, other features that are currently on can maintain an active response of the CFS stimulus, such that it continues to suppress the response to the static stimulus in the other eye.

In a similar vein, H. R. Wilson (2017) elaborated his model to explain binocular fusion with small inter-ocular differences in addition to binocular rivalry with larger differences. He proposed two types of inter-ocular inhibitory neurons. First, inhibitory interactions occur between neurons responding to features of similar spatial profiles in the two eyes, resembling the idea of within-channel masking. This is based on the notion of (logical) exclusive OR neurons put forward by Blake (1989). Wilson suggests that this kind of inter-ocular suppression is achieved by contrast normalisation. The second type which is optimally stimulated by a given feature in one eye, inhibits the response of neurons to very different features in the other eye (cf. cross-channel masking; see Figure 1.22). The putative inhibitory interactions undergo self-adaptation to generate perceptual alternations as proposed in H. R. Wilson's (2007) original model. However, this latter type of inhibition is switched off by the activity of the first type of inhibitory neurons—when there are matched features in the two eyes. A similar idea

has been incorporated into Said and Heeger's (2013) model that, amongst other things, accounts for the lack of rivalry with a binocular plaid stimulus (see Figure 1.8).

1.8 Individual differences

A key unresolved issue in this area concerns the underlying sources of the large individual differences found in the susceptibility to inter-ocular suppression, both in terms of clinical suppression (e.g. Holopigian, Blake, & Greenwald, 1988) and laboratory-induced suppression in normal binocular vision (e.g. Brascamp, Qian, Hambrick, & Becker, 2019).

In the literature on binocular rivalry, individual differences have been frequently noted, both in terms of the depth of suppression measured as a reduction in sensitivity (Alais et al., 2010) and also in terms of the temporal dynamic measures, with respect to phase duration (Bosten et al., 2015; Carter & Pettigrew, 2003; Dieter, Sy, & Blake, 2017b; Law, Miller, & Ngo, 2017; Patel, Stuit, & Blake, 2015; van Loon et al., 2013), alternation rate (Carter & Pettigrew, 2003; Dieter et al., 2017b; Fesi & Mendola, 2015; Hancock, Gareze, Findlay, & Andrews, 2012; Kleinschmidt, Sterzer, & Rees, 2012; Law et al., 2017; Miller et al., 2010), and local biases in the visual field (Dieter, Sy, & Blake, 2017a). These individual differences in BR appear to be, in part, predictable from other aspects of visual and cortical functioning including cortical surface area (Genç, Bergmann, Singer, & Kohler, 2013), gamma-amino-butyric acid (GABA) concentration (van Loon et al., 2013), peak frequency of Gamma activity in visual cortex (Fesi & Mendola, 2015), frequency of saccadic eye movements (Hancock et al., 2012), dynamics of other perceptual rivalry paradigms (Brascamp et al., 2019; Cao, Wang,

Sun, Engel, & He, 2018; Carter & Pettigrew, 2003; Patel et al., 2015), and genetic factors (Miller et al., 2010). Importantly, the high intra-individual reliability of some of these measurements indicates that they are unlikely to be due to measurement error (Genç et al., 2013; Miller et al., 2010).

Individual differences in CFS is also evident in past research, both with respect to suppression duration (Gayet & Stein, 2017; Moors et al., 2015; Yamashiro et al., 2014; Yamashiro et al., 2009; E. Yang, Blake, & McDonald, 2010) and depth of suppression as measured by a reduction in sensitivity (Hong & Blake, 2009; Ledgeway et al., 2013; Maehara et al., 2009; Zadbood et al., 2011). Neuroimaging studies have sought to identify the neural substrates associated with individuals' susceptibilities to CFS. Suppression duration has been shown to be correlated with an individual's fMRI activity in extrastriate visual areas (Yamashiro et al., 2014; Yamashiro et al., 2009). It has also been noted that intra-individual variability of suppression under CFS as a function of stimulus attributes (i.e. slope of the modulation), seems to predict an individual's susceptibility to suppression (Gayet & Stein, 2017; Ledgeway et al., 2013). For example, the more an individual was susceptible to suppression evoked by CFS in general, the more evident dependence of suppression on the contrast of the CFS stimulus or the inter-ocular luminance difference was observed (Figure 1.23). These results imply that inter-individual variation in CFS is feature dependent. In addition, the differences between individuals, when measured in the absence of CFS, do not predict those measured under CFS (Gayet & Stein, 2017). Based on these findings, it seems that individual differences in CFS may reveal crucial aspects of its underlying mechanisms, particularly about its relationship with similar phenomena where substantial individual differences are also present.

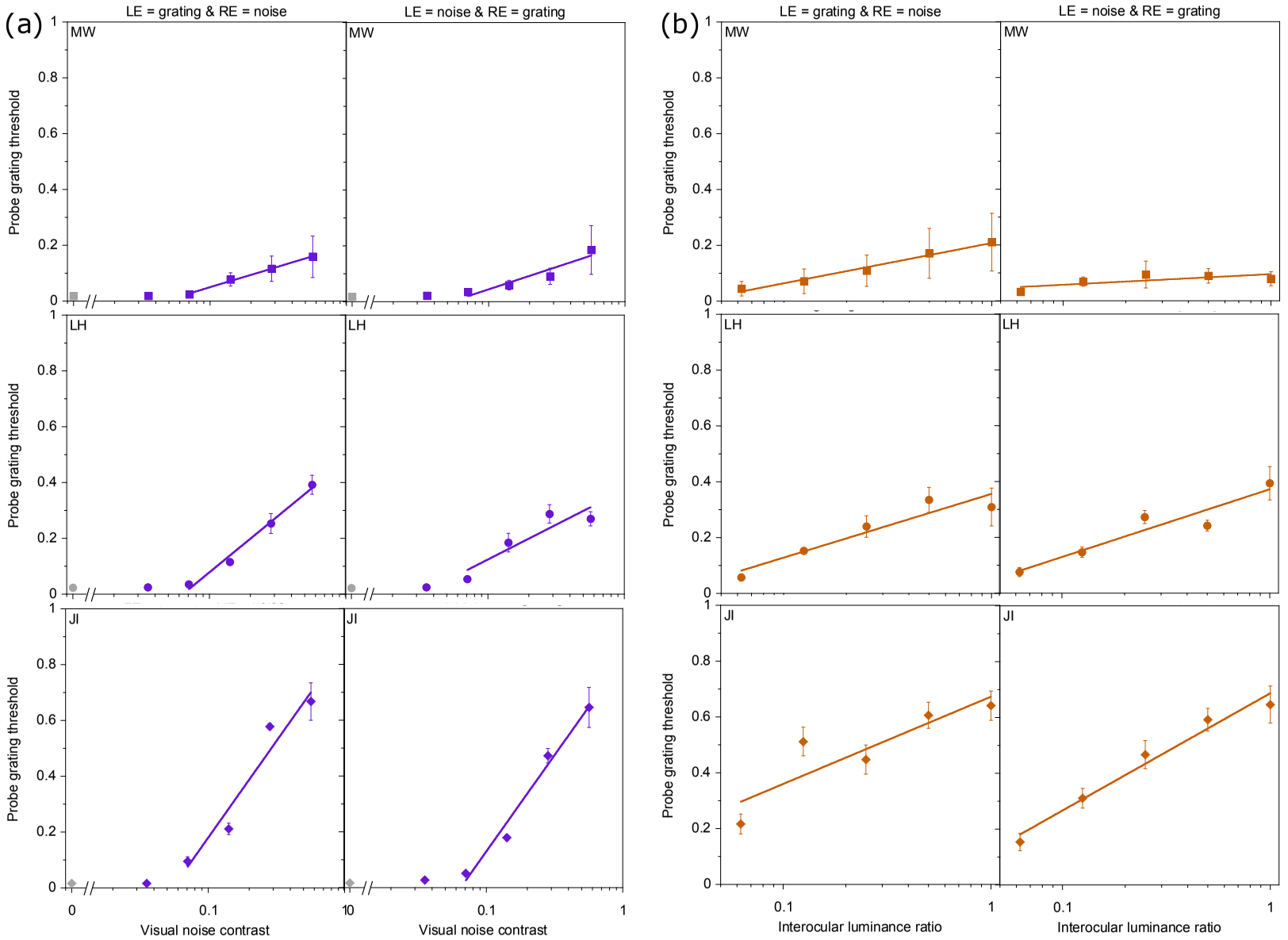

(a)
LE = grating & RE = noise
LE = noise & RE = grating
MW
LH
JI
Probe grating threshold
Visual noise contrast
(b)
Interocular luminance ratio

Figure 1.23 *(previous page)*: The dependence of contrast increment threshold under CFS on the contrast of the flashing stimulus (a) or the inter-ocular luminance ratio (b) for three observers. The higher the contrast of the CFS stimulus (i.e. dynamic visual noise), or the higher its luminance relative to that of the target, the higher the threshold for detecting contrast increment in the target (i.e. probe). The data are shown for the thresholds measured in the left eye or the right eye. Note the evident individual differences, both in terms of the susceptibility to suppression in general, and the degree of dependence on contrast or relative luminance (i.e. slope). Unpublished data from an earlier project conducted by the author (M. Wang) and others.

However, most research into CFS has not explicitly explored individual differences and their potential causes, by typically pooling data across subjects, normalising data, or removing data from subjects showing insufficient suppression (e.g. Shui'Er Han et al., 2019). Only very recently[8], has a study directly investigated the correlation between individual differences measured in BR and CFS (Blake, Goodman, Tomarken, & Kim, 2019). The measure of suppression adopted in that work, however, was temporal dynamics, which may be problematic as a meaningful metric of suppression depth (see Section 1.5). Therefore, the conclusion drawn by Blake et al. (2019) may be limited in what it can tell us about the relationship between the depth of suppression evoked by BR and CFS.

1.9 Inter-ocular latency differences

The temporal difference between the processing of two eyes' signals is believed to be a crucial factor in many aspects of binocular vision, such as stereopsis (Read & Cumming, 2005). The significance of inter-ocular delay may also apply to the strength of inter-ocular suppression.

Kaunitz et al. (2014) showed that the effectiveness of inter-ocular sup-

[8]At the time when this thesis was being written.

pression evoked by CFS degraded as the delivery of the flashing mask and the target stimulus became more asynchronous. In a similar vein, Tsuchiya et al. (2006) revealed that depth of suppression under either BR or CFS was tuned to the temporal alignment of the suppressing and the target stimuli (i.s. stimulus onset asynchrony, SOA). Moreover, the depth of suppression under CFS decreased as the luminance of the flashing stimulus was lowered relative to that of the target (see Figure 1.23b; Ledgeway et al., 2013). It is well established that decreasing the luminance of a stimulus slows its visual processing (J. A. Wilson & Anstis, 1969). Therefore, it is possible that the reduced inter-ocular suppression found was a consequence of a temporal lag between the two eyes' images, which was introduced by lowering one eye's luminance.

It is also worth noting in amblyopia that the visual processing of the amblyopic eye's input is supposedly delayed compared to that in the fellow eye (Chadnova, Reynaud, Clavagnier, & Hess, 2017a; Farivar, Thompson, Mansouri, & Hess, 2011; Gambacorta, Ding, McKee, & Levi, 2018; McKee, Levi, Schor, & Movshon, 2016), and that the inter-ocular suppression elicited by the amblyopic eye is weak (Ding, Klein, & Levi, 2013a; Huang, Baker, & Hess, 2012; Shooner et al., 2017; Zhou et al., 2018). This raises the possibility that the optimal timing relationship between the flashing and the target stimuli to trigger suppression may vary among people, and that in turn could potentially explain the marked inter-individual variation in susceptibility to CFS suppression existing in the general population. This proposal has not yet been directly tested but remains a fruitful avenue for future investigation into individual differences in suppression depth.

1.10 Eye dominance

The susceptibility to inter-ocular suppression appears to vary not only across individuals, but also between eyes for an individual (Dieter et al., 2017a; Ding et al., 2013a; T. Y. Gao et al., 2016, 2018; C. Han, He, & Ooi, 2019; Maehara et al., 2009; Zhou et al., 2018). That is, there is a bias in some individuals where one eye is more susceptible to suppression by the other eye than vice versa. This reveals different contributions of the two eyes to binocular interactions in those individuals. In fact, sensory eye dominance is a prominent feature of amblyopia, and is possibly related to reduced binocular function (Barrett et al., 2004; Coren & Duckman, 1975; Goodyear, Nicolle, & Menon, 2002; Porac & Coren, 1975; Schröder, Fries, Roelfsema, Singer, & Engel, 2002). Besides, sensory eye dominance (in both binocular combination and inter-ocular suppression) also exists in the general population, in the absence of known deficiency in visual functions, and has been shown to be a good predictor of stereopsis (e.g. Dieter et al., 2017a; C. Han, He, & Ooi, 2018, 2019). Notably, absolute differences in monocular sensitivity have been shown to be insufficient to fully account for the discrepant contributions of the eyes (C. Han et al., 2018; Ooi & He, 2001; J. P. Xu, He, & Ooi, 2011), implying that the asymmetry occurs in terms of inter-ocular interactions.

Many studies of inter-ocular suppression have however averaged measurements across eyes (e.g. Tsuchiya et al., 2006), or have chosen to examine only the eye that elicits the higher level of suppression (e.g. Yamashiro et al., 2014; Yuval-Greenberg & Heeger, 2013), which may obscure asymmetries between the two eyes' susceptibilities to suppress or be suppressed. For this reason, it is vitally important in future studies to measure suppres-

sion independently in the two eyes to avoid overlooking important features of sensory eye dominance.

In this context, tasks of BR (Dieter et al., 2017a; C. Han et al., 2018; Lunghi, Burr, & Morrone, 2011; Lunghi, Burr, & Morrone, 2013) and CFS (E. Yang, Blake, & McDonald, 2010) have both been utilised as protocols of assessing sensory eye dominance. However, there exist inconsistencies between different measurements in terms of the eye which is considered dominant (Dieter et al., 2017a; C. Han et al., 2018; Handa et al., 2004; Ooi & He, 2001; E. Yang, Blake, & McDonald, 2010). It is thus interesting to ask whether the sensory eye dominance measured with BR agrees with that measured under CFS. A common pattern of eye dominance is expected if CFS is for example simply a stronger version of BR without any qualitative differences.

1.11 Short-term monocular deprivation on sensory eye dominance

Neural plasticity has been extensively studied in mammalian visual systems and is a prominent feature of developing brains. If exposed to abnormal visual input during development, structural and functional changes are induced in visual cortex, presumably driven by mechanisms for maintaining an adaptive and stable environment in the brain (Keck et al., 2017; Turrigiano & Nelson, 2000). A well documented example is the shift in ocular dominance induced by monocular deprivation (Hubel & Wiesel, 1964). Prolonged disruption of visual input to one eye in young animals (e.g. kittens, monkeys, mice), leads to a weakened responsiveness of the affected eye and a shrinkage of ocular dominance columns associated with that eye (F. H.

Baker, Grigg, & von Noorden, 1974; Blakemore, Garey, & Vital-Durand, 1978; Crawford, Blake, Cool, & von Noorden, 1975; Frenkel & Bear, 2004; Hubel, Wiesel, & LeVay, 1977; Le Vay, Wiesel, & Hubel, 1980; Wiesel & Hubel, 1963). These changes are specific to imbalanced input, since deprivation of both eyes together does not produce the same effects (Crawford et al., 1975; Wiesel & Hubel, 1965). The shift in ocular dominance, nonetheless, can be reversed by subsequently depriving the previously open eye, although the effectiveness of this reversal is restricted to a critical time window (Blakemore et al., 1978; Swindale, Vital-Durand, & Blakemore, 1981). Interestingly, recent research in human adults has demonstrated effects of short-term monocular deprivation in the opposite direction, that sensory eye dominance is shifted in favour of the previously deprived eye (Lunghi et al., 2011; Lunghi et al., 2013).

In a series of studies, Lunghi and others covered one eye of participants using a translucent lens for 2.5 hours, depriving it of spatial information but matching average luminance to that of the other eye. Sensory eye dominance was subsequently measured (after patch removal) using a BR perceptual tracking task and revealed that the patched eye dominated perception for longer periods (Figure 1.24). Coupled with behavioural changes, physiological evidence has shown increased and decreased cortical responsiveness associated with the deprived eye and the non-deprived eye, respectively (Binda et al., 2018; Chadnova, Reynaud, Clavagnier, & Hess, 2017b; Lunghi, Berchicci, Morrone, & Di Russo, 2015; Zhou, Baker, Simard, Saint-Amour, & Hess, 2015). Notably, an opaque eye patch which eliminates all visual input is also able to bias subsequent binocular balance towards the patched eye (Chadnova et al., 2017b; Zhou, Clavagnier, & Hess, 2013), whereby one may argue for a role of retinal adaptation to light. However,

the comparable effects induced by these two forms of deprivation preclude this possibility.

1.11.1 Time scale

An important aspect of sensory eye dominance plasticity following short-term monocular deprivation concerns the time scale of this phenomenon, which is perhaps one of the key parameters that make it fundamentally different from conventional monocular deprivation (e.g. Iny, Heynen, Sklar, & Bear, 2006; Pham et al., 2004; Prusky, Alam, & Douglas, 2006; Sato & Stryker, 2008; Tagawa, Kanold, Majdan, & Shatz, 2005). This is in terms of both the effect lifetime and the deprivation duration necessary to induce the plastic changes.

Lunghi et al. (2013) have shown that the altered eye dominance decayed over time and the temporal dynamics of rivalry returned to pre-deprivation levels approximately 15–30 minutes after uncovering the eye when tested with achromatic stimuli (see Figure 1.24 and Figure 1.25). The short-lived lifetime of the effect implies an absence of structural changes. This is in stark contrast to the long-term influence following extensive periods of monocular deprivation, applied early in life during critical period, that could be permanent or semi-permanent (Blakemore et al., 1978; Dews & Wiesel, 1970; Olson & Freeman, 1980; Swindale et al., 1981).

Therefore, one of the critical differences between long-term and short-term consequences on ocular dominance possibly lies in whether the deprivation is sufficiently severe (in this case, the length of period) such that some anatomical changes may occur[9]. When monocular deprivation is intro-

[9]Note that the anatomical changes following extensive periods of monocular deprivation are however limited to a critical time window (Blakemore et al., 1978; Swindale et al., 1981).

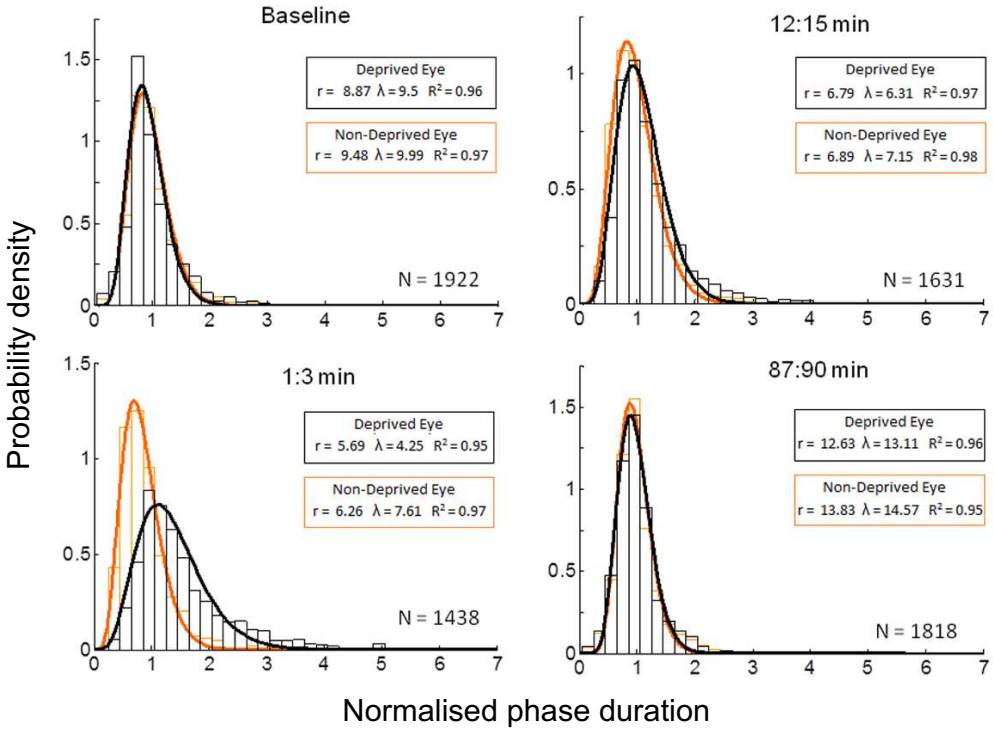


Figure 1.24: The effects of 150-minute monocular deprivation on the distributions (probability density functions) of normalised exclusive phase durations measured with a perceptual tracking task, during continuous experience of binocular rivalry (induced by achromatic stimuli). The distributions for the stimulus presented to the previously deprived eye are shown in black and those for the non-deprived eye are in orange. The upper left panel shows the data obtained prior to monocular deprivation (i.e. baseline). Within 3 minutes after removing the eye patch (lower left panel), the distribution for the deprived eye has been shifted to the right, indicating lengthened phase durations on average, while it has been slightly shifted to the left for the non-deprived eye. At 12 minutes after the end of monocular deprivation (upper right panel), the effect on phase durations has largely diminished and the distributions started to resemble those measured before deprivation. Finally, the distributions for both eyes returned to the baseline levels at 87 minutes after removing the patch (lower right panel). In every case, these phase durations can be well characterised by a two-parameter (ρ, λ) gamma function (black and orange continuous curves), and the estimated parameters are shown in the insets. Adapted from Lunghi et al. (2013).

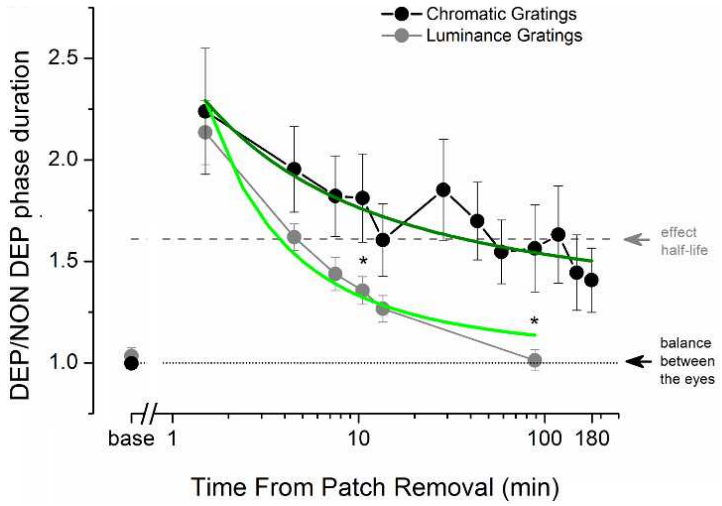


Figure 1.25: The time course of the effect of 150-minute monocular deprivation in Lunghi et al.'s 2013 study. The figure plots the ratio of deprived to non-deprived eye phase duration as a function of the time since patch removal, when either chromatic or achromatic stimuli were tested. Adapted from Lunghi et al. (2013).

duced using brief periods, purely physiological changes take place instead. In that case, it is the modified strength of neuronal activity at some stage(s) that leads to the changed eye dominance. For example, one possibility is that the contrast gain of each eye's signal is altered (see Section 1.11.2). Alternatively, if the monocular contrast gain remains unaffected as indicated by some observations (Baldwin & Hess, 2018; Lunghi et al., 2011), the modifications are likely to be at the level of inter-ocular interactions.

The length of deprivation not only seems to determine the nature of changes in eye dominance, but also can influence the lifetime of the short-term effects. The effects observed by Lunghi and colleagues in their original studies (2011, 2013), which lasted 15 minutes for achromatic stimuli and at least 180 minutes for chromatic stimuli (Figure 1.25), were produced by hours-long (150 minutes) deprivation. In fact, it has been shown that the increase in the relative dominance of the deprived eye can be effectively achieved with a deprivation duration ranging from several minutes to hours

(Kim, Kim, & Blake, 2017; Min, Baldwin, Reynaud, & Hess, 2018). Nevertheless, when Lunghi et al. (2013) used a shorter deprivation duration of 30 minutes instead, the effects lasted for only 3 minutes (Figure 1.26). It is not surprising that the effect lifetime increases with the patching duration, though a recent study has revealed that the strengthening of the patching effect by lengthening the deprivation period is modest when both the magnitude and lifetime are taken into account (Figure 1.27; Min et al., 2018).

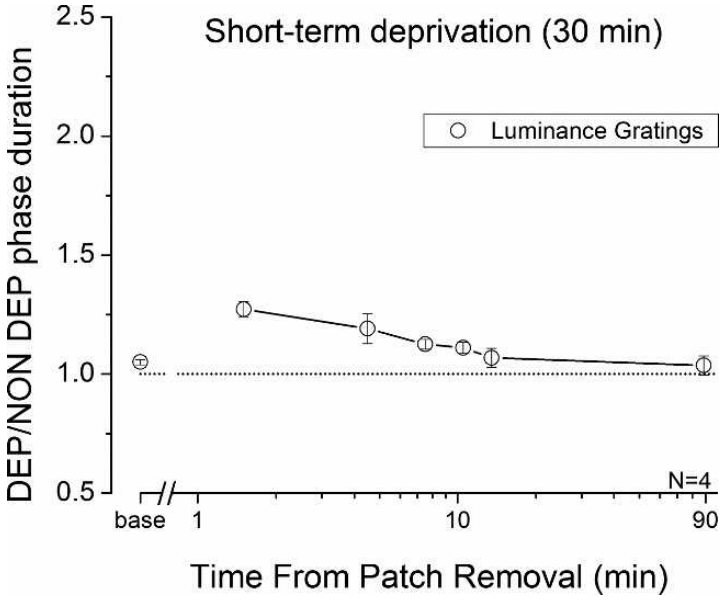


Figure 1.26: The time course of the effect of 30-minute monocular deprivation in Lunghi et al.'s 2013 study. The figure is plotted in the same manner as in Figure 1.25 but only achromatic stimuli were tested. Adapted from Lunghi et al. (2013).

1.11.2 Are shifts in sensory eye dominance driven by monocular changes?

If the previously deprived eye becomes more sensitive, and/or the other eye becomes less sensitive following monocular patching, the relative perceptual

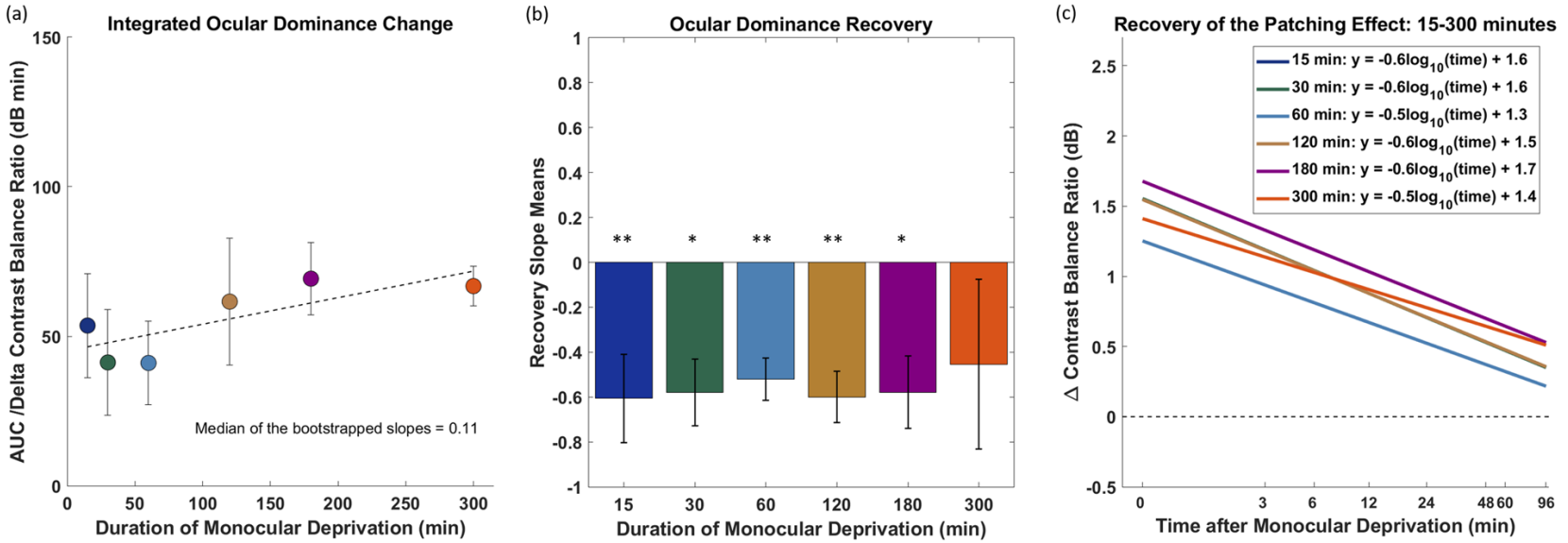


Figure 1.27: The dependence of deprivation effect on the length of deprivation. Sensory eye dominance was indicated by the contrast balance ratio measured with a binocular phase combination task (see Figure 1.29a), whereby a ratio greater than 1 indicates dominance in favour of the deprived eye. Delta contrast balance ratio refers to the difference between the ratio measured following monocular deprivation and that before deprivation, such that higher values indicate larger shifts towards the deprived eye. (a) Area under curve (AUC) for the decay time course of the delta contrast balance ratio following various durations (15–300 minutes) of monocular deprivation, which quantifies the deprivation effect considering both magnitude and lifetime. (b) The corresponding slopes of the decay functions. (c) The delta contrast balance ratio as a function of the time from patch removal for a subset of deprivation duration conditions (60–300 minutes). Adapted from Min et al. (2018).

contribution of each eye to binocular tasks will be changed accordingly. However, evidence for this proposal is mixed. In Lunghi et al.'s (2011) original study, no change in each eye's contrast discrimination threshold was found following monocular deprivation. This was also the case in later studies (e.g. Baldwin & Hess, 2018). In addition to the direct observations of unchanged monocular sensitivity[10], indirect evidence can be inferred from the results by Baldwin and Hess (2018). They showed that the size of the deprivation effect, revealed with different binocular tasks, was not significantly correlated with each other across subjects (Figure 1.28). A correlation would be expected if the changes in binocular balance were underpinned by a single effect such as altered monocular sensitivity following patching. On the other hand, other work has shown lowered monocular detection thresholds in the previously deprived eye along with elevated thresholds in the non-deprived eye; consequently these authors suggested that the shifts in eye dominance result from changes in monocular contrast gain of each eye (Zhou, Clavagnier, & Hess, 2013; Zhou, Reynaud, Kim, Mullen, & Hess, 2017; Zhou, Thompson, & Hess, 2013).

The inconsistencies in results might be related to different types of thresholds being measured (e.g. discrimination vs. detection). Nevertheless, the number of subjects tested in previous studies was limited (e.g. 2 subjects in Zhou, Clavagnier, and Hess's (2013) study), and the magnitude of effects was small.

Therefore, the findings regarding whether monocular sensitivity is systematically affected by short-term monocular deprivation appear currently inconclusive and require further examination.

[10]Lunghi et al. (2011) measured contrast discrimination thresholds, and Baldwin and Hess (2018) measured contrast detection thresholds (but only in pilot testing).

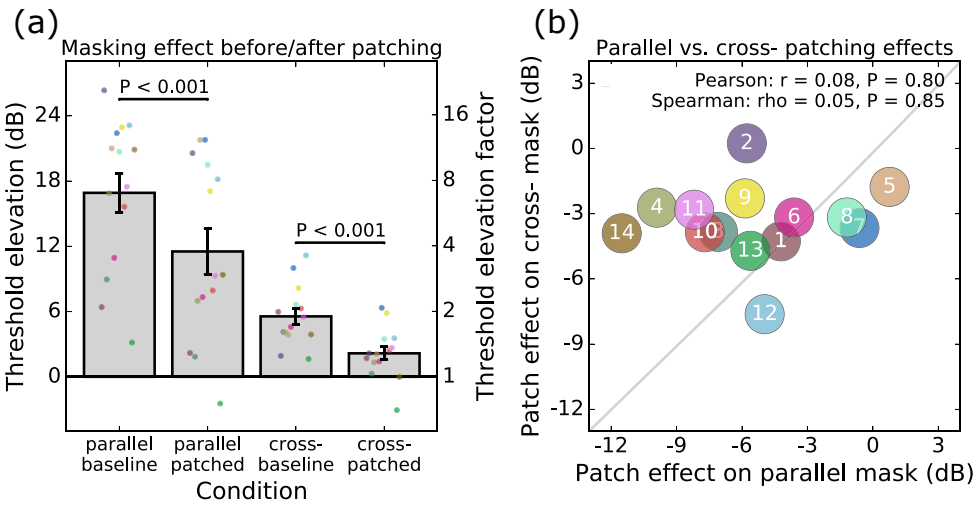


Figure 1.28: Dichoptic masking following short-term monocular deprivation. (a) For both parallel (the mask and the target had identical orientations) and cross-orientation (the mask and the target had orthogonal orientations) dichoptic masking, 150-minute monocular deprivation significantly reduced subsequent masking effect (indicated by threshold elevation) of the previously patched eye. (b) The patching effect, indexed by the reduction in the masking effect of the previously patched eye, was not significantly correlated between parallel and cross-orientation masking across the group of participants tested. Adapted from Baldwin and Hess (2018).

1.11.3 Does short-term monocular deprivation affect integrative and inhibitory binocular interactions in the same way?

In addition to measuring rivalry, other work has used tasks requiring integration of binocular inputs to quantify changes in sensory eye dominance (Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013). This is based on the assumption that the combined binocular percept is a product of the summation of weighted gain from each eye's input (Ding & Sperling, 2006). One of these studies observed an increased relative contribution of the deprived eye, measured using binocular phase combination and binocular contrast matching tasks (Figure 1.29; Zhou, Clavagnier, & Hess, 2013), consistent with Lunghi and coworkers' results revealed with rivalry dynamics. However, when the phase information presented to one eye was scrambled (a form of monocular phase deprivation) different effects were found depending on the task used to measure sensory eye dominance (Bai, Dong, He, & Bao, 2017; Zhou, Reynaud, & Hess, 2014). When a rivalry task was used, the pattern of results was consistent with previous work (Bai et al., 2017). However, for a binocular combination task, there was no change in eye balance (Bai et al., 2017; Zhou et al., 2014). This raises the possibility that there are multiple mechanisms involved in the plasticity of sensory eye dominance; contrast combination between fusible stimuli, and binocular rivalry between incompatible stimuli, are differentially affected by monocular deprivation.

A recent study has revealed a lack of relationship between the deprivation effects on different binocular processes despite using similar measures (Figure 1.28; Baldwin & Hess, 2018). In Baldwin and Hess's (2018) study,

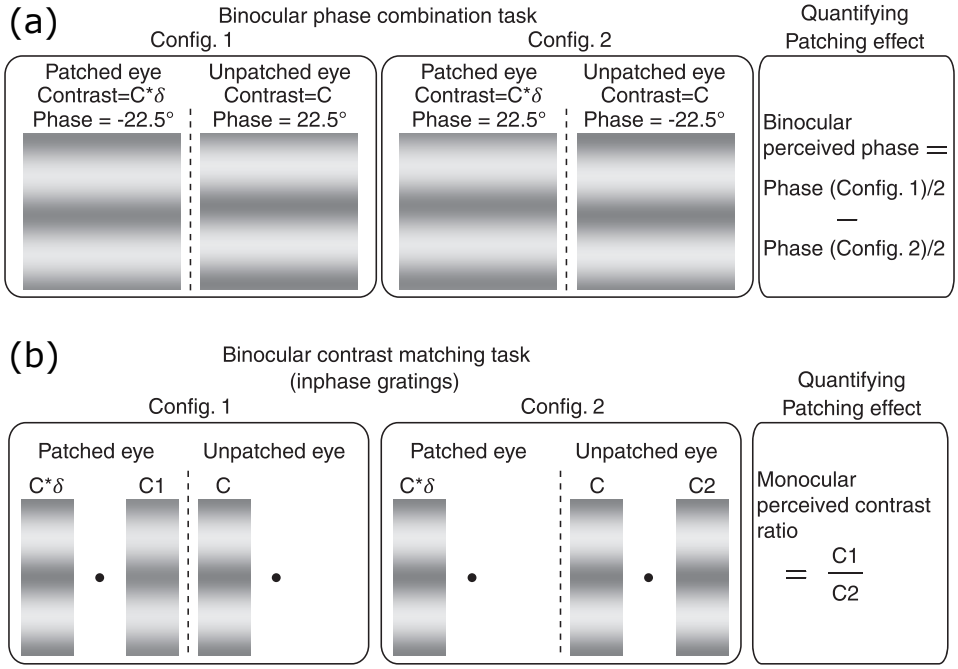


Figure 1.29: Tasks requiring integration of visual inputs from the two eyes used by Zhou, Clavagnier, and Hess (2013) to quantify sensory eye dominance. (a) Binocular phase combination task. Two horizontally-oriented sine-wave gratings are presented to the two eyes dichoptically. The spatial phase of gratings are offset by 45 degrees (+22.5 degrees in one eye and –22.5 degrees in the other eye). When combined binocularly the perceived phase supposedly depends on each eye's contrast gain. When the contributions of the two eyes are equal, the perceived phase is expected to be the average of the two gratings' phases (0 degree). When the contribution of one eye is greater than that of the other eye, the perceived phase is biased towards the phase of the grating presented to the former. Thereby, the degree of sensory eye dominance is indicated by such a bias. (b) Binocular contrast matching task. The apparent contrast of the stimulus presented to each eye is measured by requiring the participant to match the contrast of a monocular stimulus (presented in the eye of interest) to a standard stimulus that is presented binocularly. The stimuli used are typically horizontally-oriented sine-wave gratings, where the binocular standard is presented on one side of the fixation and the monocular test stimulus is presented on the other side. Sensory eye dominance is quantified by comparing the apparent contrast measured in the two eyes. Adapted from Zhou, Clavagnier, and Hess (2013).

the effect of short-term monocular deprivation was assessed with two variations of dichoptic masking, when the orientations of the two eyes' stimuli were the same (i.e. parallel condition) and when they were very different (i.e. cross-orientation condition). Their results showed a reduction in masking effects on the deprived eye in both conditions, but that the individual differences in magnitude of this deprivation effect revealed in the two tasks were not correlated. Based on the binocular fusibility of stimuli, Baldwin and Hess (2018) proposed a mechanistic link between parallel dichoptic masking and binocular contrast combination, and between cross-orientation dichoptic masking and binocular rivalry. This again makes it reasonable to question whether a common mechanism of plasticity underpins changes in integrative and inhibitory binocular interactions.

1.11.4 Relevance to amblyopia

Plasticity in ocular dominance has a great bearing on both the development and treatment of amblyopia, which is typically characterised by impaired binocular functions (Barrett et al., 2004; Crawford & Harwerth, 2004). Monocular deprivation has been frequently utilised as a protocol to induce amblyopia in young animals (e.g. von Noorden, 1973; von Noorden, Dowling, & Ferguson, 1970), because the condition is believed to be often a consequence of disrupted inter-ocular correlation that leads to the suppression of one eye[11] (Harrad, Sengpiel, & Blakemore, 1996). On the other hand, short-term monocular deprivation (in the form of part-time occlusion) of the unaffected eye is the cornerstone of treatment for human amblyopia in childhood (Campos, 1995; Webber, 2007; Webber & Wood,

[11]This possibility is ecologically conceivable as there is a need for an efficient solution to the persistent conflict in the visual input.

2005), which is reminiscent of the recovery of binocularity by reversal deprivation (Blakemore et al., 1978; Swindale et al., 1981). For both phenomena, the plastic changes appear to be limited to developing visual systems prior to the closure of a critical period of visual development (Blakemore et al., 1978; Blakemore & van Sluyters, 1974; Dews & Wiesel, 1970; Epelbaum, Milleret, Buisseret, & Duffer, 1993).

It seems that the severity of perceptual deficits and inter-ocular acuity differences in amblyopia are associated with the degree of inter-ocular suppression (Holopigian et al., 1988; J. Li et al., 2011; Sireteanu & Fronius, 1981). Crucially, there is evidence indicating asymmetric suppression of the two eyes in amblyopia (Barrett et al., 2004; Ding et al., 2013a; Huang et al., 2012; Shooner et al., 2017; Zhou et al., 2018). It is therefore worth asking whether short-term monocular deprivation is able to alter sensory eye dominance in terms of susceptibility to inter-ocular suppression, which may shed important light on patching therapies of amblyopia. Although the effects of short-term monocular deprivation appear to be temporary, previous studies have hinted at a potential link between the transient homeostatic plasticity involved and long-term recovery of visual acuity in adult amblyopia (Lunghi, Morrone, Secci, & Caputo, 2016; Lunghi et al., 2019; Zhou et al., 2019).

It is generally considered that inter-ocular suppression is involved in BR (e.g. Sengpiel et al., 1995), but the deep unilateral suppression produced by CFS may be more relevant to (or a better model of) the persistent inter-ocular suppression found in strabismic amblyopia, which is thought to prevent diplopia or confusion (Barrett et al., 2004; Harrad et al., 1996). As pointed out in Section 1.10, CFS can be used as an alternative paradigm for characterising the sensory balance between eyes. Therefore there is a clear

need to investigate the effect of short-term monocular deprivation on each eye's susceptibility to CFS to shed light on this issue.

1.11.5 Does the type of monocular deprivation matter?

In the first series of studies conducted by Lunghi and colleagues (2011, 2013), a translucent lens was chosen to filter out the form information—the eye was not deprived of light. The reason behind this may be that differences in luminance convey more information than absolute luminance (De Valois & De Valois, 1988; Snowden, Thompson, & Troscianko, 2012). Selective elimination of certain classes of visual information is also feasible with some techniques. Comparing the effects induced by various forms of deprivation can provide some insights into the mechanisms responsible for the modulation of sensory eye dominance.

For instance, a study by Chadnova et al. (2017b) used both a translucent lens and an opaque patch, and demonstrated shifts in the relative dominance towards the deprived eye following either type of patching measured with magnetoencephalography (MEG). Behaviourally, Zhou, Clavagnier, and Hess (2013) observed comparable enhancement of the deprived eye produced by these two types of deprivation using a binocular phase combination task[12].

In addition to occluding one eye, there are variants of monocular deprivation that only eliminate or attenuate a specific element of visual informa-

[12]Nevertheless, as already addressed in Section 1.11.3, it is difficult to generalise the results obtained with tasks requiring binocular integration to patterns of inter-ocular suppression where sensory eye dominance manifests in each eye's contribution to inhibitory binocular interactions. Therefore, whether translucent and opaque patching have similar effects on sensory eye dominance measured with inter-ocular suppression such as BR and CFS remains unknown.

tion. For example, by selectively eliminating contours of a given orientation from the visual input to one eye, Zhou et al. (2014) have demonstrated a subsequent shift in eye dominance favouring the treated eye, in human observers, measured with stimuli only containing non-deprived orientations (Figure 1.30; see also Y. Wang, Yao, He, Zhou, & Hess, 2017). That is to say, the changes in eye dominance were not limited to the deprived orientations. Similar conclusions were also obtained in a physiological study that recorded the V1 neurons of adult macaques using intrinsic signal optical imaging (Begum & Tso, 2016). This finding led Zhou et al. (2014) to conclude that the neurons in layer $4C_B$ of V1 are responsible for sensory eye dominance plasticity following short-term monocular deprivation as they respond to the stimulation of both eyes (i.e. binocular neurons) and at the same time are not selective to orientation. From this work it is evident that experiments on selective deprivation may provide important insight into the mechanisms underpinning such plasticity.

Some work has also selectively disrupted phase regularity in one eye, to explore whether this parameter is important for the modulation of sensory eye dominance. The images viewed by one eye were scrambled in Fourier phase with amplitude unaltered, while the other eye was presented with matched but unprocessed images (Bai et al., 2017; Zhou et al., 2014). Using this monocular manipulation, a shift in dominance towards the treated eye was still found with binocular rivalry (Bai et al., 2017), but the relative contributions of the two eyes to binocular phase combination remained unchanged (see Section 1.11.3; Bai et al., 2017; Zhou et al., 2014). This implies that (spatial) inter-ocular correlation plays an essential role in the regulation of sensory eye dominance in terms of the contribution to inhibitory, but not integrative, binocular interactions.

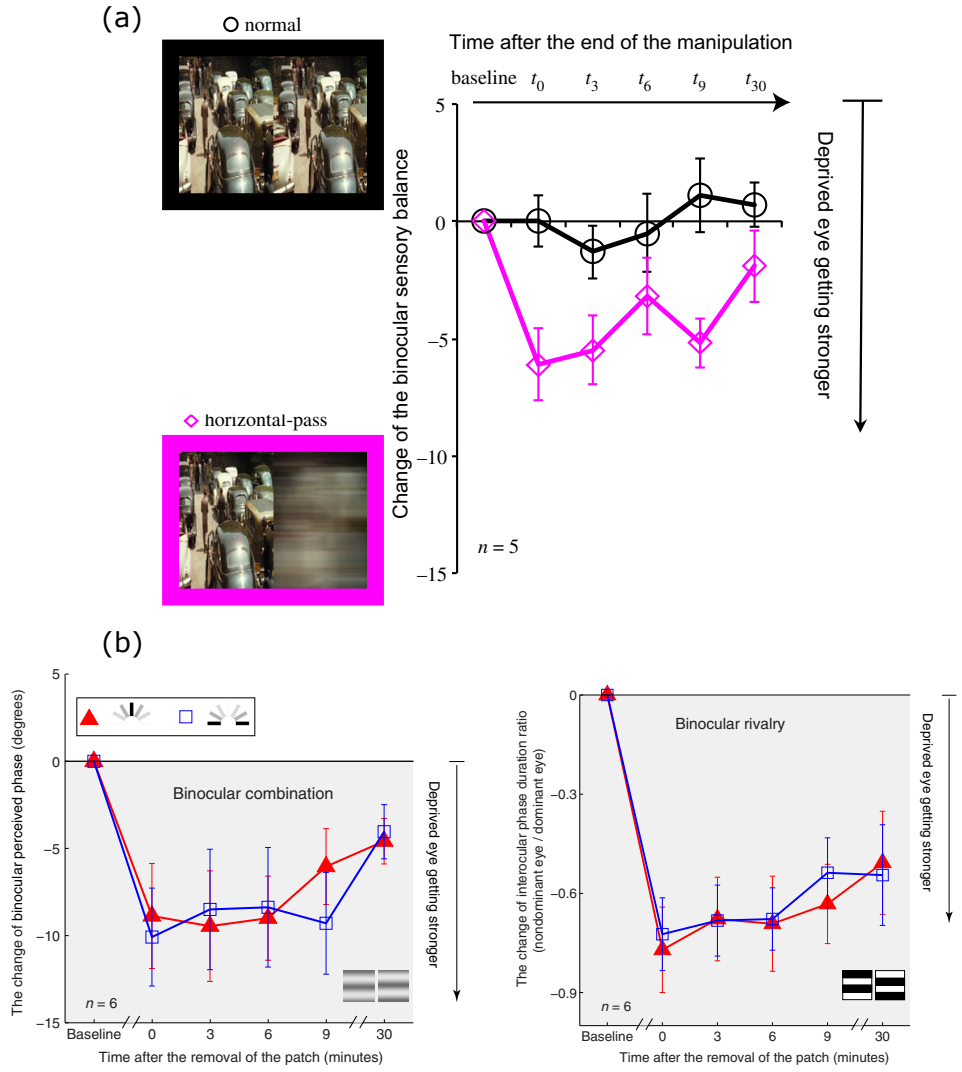


Figure 1.30: Orientation non-selectivity of the effects of short-term monocular deprivation on sensory eye dominance. (a) When one eye's images were filtered to contain only horizontal information for 2.5 hours (the other eye viewed normal images), subsequent eye dominance was shifted towards the treated eye, measured using a binocular phase combination task (see Figure 1.29a) where stimuli were horizontally-oriented sine-wave gratings. Adapted from Zhou et al. (2014). (b) When one eye was selectively deprived of either horizontal (triangles) or vertical information (squares), subsequent eye dominance measured with stimuli only containing horizontal information was shifted towards the treated eye, in both a binocular phase combination task (left panel) and a binocular rivalry task (right panel). Adapted from Y. Wang et al. (2017).

By using different types of monocular manipulation, two general factors are revealed that may play a crucial role in the modulation of sensory eye dominance. First, it may be the inter-ocular imbalance *per se* that leads to subsequent shifts in eye dominance. For example, evidence suggests that the mere reduction in contrast of a monocular image is able to increase the relative dominance of the treated eye, despite the fact that the two eyes' images are still highly correlated and fusible (Kim et al., 2017; Zhou et al., 2014). Second, inter-ocular correlation may also be relevant. It is plausible that sensory eye dominance is affected by disrupting the use of the two eyes together. Yet, as the shift in eye dominance is in a given direction (i.e. enhancement of one eye rather than the other), there must be another factor that determines which eye becomes more dominant following the disruption of inter-ocular correlation. Therefore, this is usually realised by distorting one eye's image while keeping the other eye's image unaltered (e.g. Bai et al., 2017; Zhou et al., 2014). As mentioned in the last paragraph, with monocular distortion shifts in eye dominance can be observed under some conditions, but it also seems to depend on the tasks adopted (Bai et al., 2017; Zhou et al., 2014). Furthermore, Kim et al. (2017) have illustrated that a lack of conscious awareness in one eye produced by inter-ocular suppression is able to bias subsequent eye dominance, favouring the previously suppressed eye. Although disrupted inter-ocular correlation is likely to play a role in that situation, it raises the possibility that other higher-level factors beyond the distortion of low-level visual input, may also contribute to the shifts in eye dominance, when they induce a difference between the processing of the two eyes' information.

1.12 Top-down attentional modulation

Under conditions of conflicting visual input between the two eyes, the brain has to resolve this ambiguity and select only one image to be perceived. This selection process is reminiscent of another prominent feature of the visual system, namely, attention (Allport, 1989; Reynolds & Chelazzi, 2004). The relationship between attention and BR has long been of interest to rivalry scholars, and a substantial overlap in the cortical networks involved in the two processes points to a close link (Leopold & Logothetis, 1999; Paffen & Alais, 2011). Before discussing this topic, it is necessary to clarify that there are two types of attention that may influence BR. Whilst exogenous attention refers to a bottom-up process whereby attention is automatically directed to a salient stimulus, the present discussion will primarily focus on endogenous attention that involves top-down, voluntary control (see Posner, 1980).

A long-standing debate has been whether BR is subject to the control of endogenous attention. A strong impact of voluntary attention on perception under conditions of BR was reported by von. Helmholtz (1925), in that he could wilfully control what was to be perceived. However, Breese (1899) subsequently argued that peripheral mechanisms (i.e. not cortical) such as eye movements *per se* have led to the altered perceptual alternations (also see Peckham, 1936). Nevertheless, with the development of new techniques, later studies have shown influences of attention on BR, even after carefully controlling for eye movements (e.g. Lack, 1978). This has prompted a rethink about a lack of attentional control (e.g. W. J. M. Levelt, 1965; Moray, 1970), and subsequently received support from more recent research[13] (Meng & Tong, 2004; Van Ee, 2005).

[13]These studies showed that the participants were able to voluntarily retain the dom-

Whilst attentional control of BR can be demonstrated via the rate of perceptual alternations (Meng & Tong, 2004; Paffen, Alais, & Verstraten, 2006), it may also have a bearing on relative dominance between the two eyes. That is, selectively attending to one of the rivalrous stimuli can boost the dominance of the attended stimulus relative to the unattended one (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; Ooi & He, 1999; Zhang, Jiang, & He, 2012). Consistent with the idea of eye selection by attention, Dieter and Tadin (2011) proposed a framework suggesting that attention serves to resolve the conflict between the two eyes' visual inputs, a role analogous to the resolution of spatial conflict (Figure 1.31; McMains & Kastner, 2011). In support, Dieter et al. (2015) have demonstrated that the modulation of attention is largest during periods of BR where unresolved conflict is greatest. In this study, presenting a binocular, transient cue that had the same pattern as the dominant percept during BR increased the median dominance duration of that stimulus, whereas its duration was shortened if the cue had the same pattern as the suppressed stimulus (Figure 1.32). Crucially, this effect was eliminated when the analysis only included data where the cue onset was early rather than late during a dominance phase. It has been found previously that depth of suppression was strong immediately following a perceptual switch and decreased towards the end of the dominance phase (Alais et al., 2010). These results led Dieter et al. (2015) to conclude that an attentional cueing effect was only present if there was sufficient conflict that required resolving—when inter-ocular suppression was weak.

In addition to sensory eye dominance measured with BR, the effect of attentional control has also been demonstrated in a CFS paradigm. The

inance of a rivalrous stimulus and also to influence the rate of perceptual alterations.

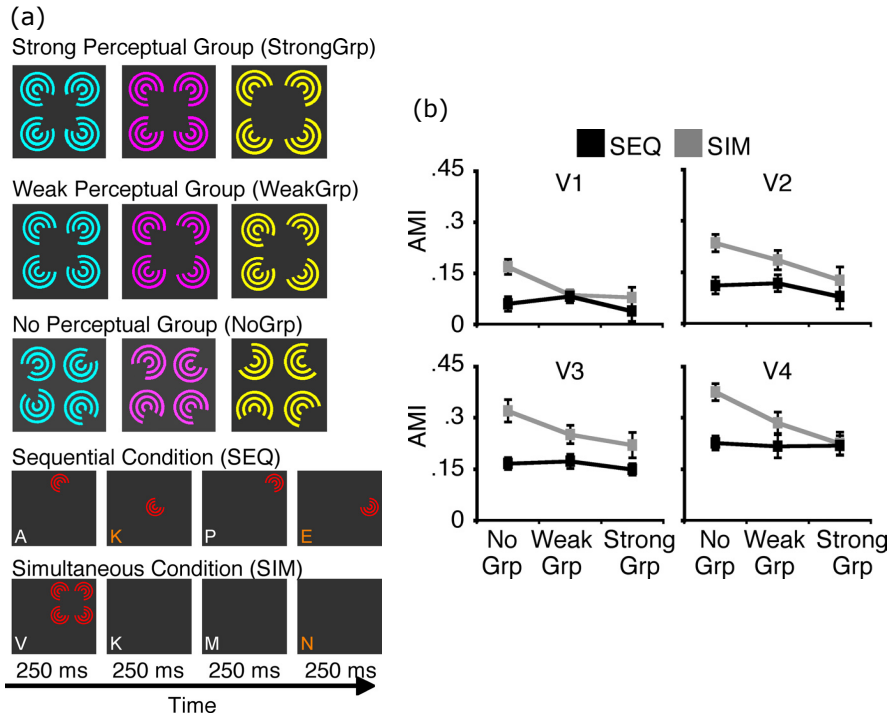


Figure 1.31: Dependence of attentional modulations in visual cortex on degree of spatial conflict. (a) The degree of spatial conflict was manipulated by varying the strength of perceptual grouping (top panel) and the temporal relationship between the elements constituting the perceptual group stimulus (bottom panel). Weaker perceptual grouping or simultaneous presentation results in a greater level of spatial conflict than stronger perceptual grouping or sequential presentation. (b) Attentional modulation index (AMI) that indicates attention-related activity changes in V1–V4. AMI decreased as the strength of perceptual grouping was increased but only in the simultaneous condition. When the stimulus elements were presented sequentially, AMI was generally lower than that in the simultaneous condition, and the dependence on perceptual grouping strength was eliminated. These results suggest that attentional modulation increases with the level of spatial conflict. Adapted from McMains and Kastner (2011).

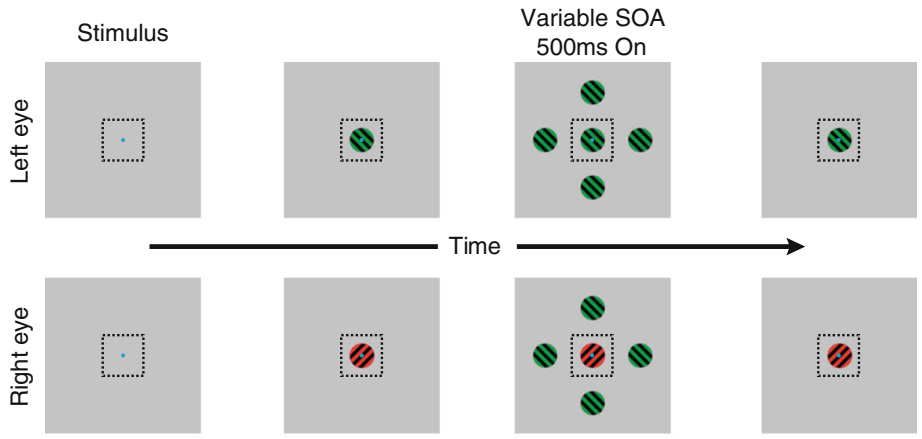


Figure 1.32: Paradigm used by Dieter et al. (2015) to show effects of attentional cueing on binocular rivalry. A transient cue was presented binocularly to surround the rivalrous stimuli (within the central square region), at a variable onset after one of the stimuli became dominant. The pattern of the cue was identical to either the dominant or the suppressed percept. Adapted from Dieter et al. (2015).

suppression time of a stimulus was reduced when attention was directed to an external cue (at a non-overlapping location in the visual space) presented to the same eye as this stimulus, compared to when the cue was presented to the other eye viewing the suppressing stimulus (Figure 1.33; Zhang et al., 2012). The finding that this effect increased with attentional load but did not depend on the low-level attributes of the cue indicates a specific role of attention. Crucially, as it was the external cue, rather than either of the conflicting stimuli that was selectively attended to, these results revealed attentional facilitation of the eye instead of the specific stimulus or spatial location. In an electroencephalogram (EEG) study, neuronal activity in early visual areas specific to the attentional modulation of eye dominance during BR was observed, which was absent when the stimulus competition occurred in only one eye (Mishra & Hillyard, 2009). This finding also underscores a role of attention in eye selection over and above pattern selection.

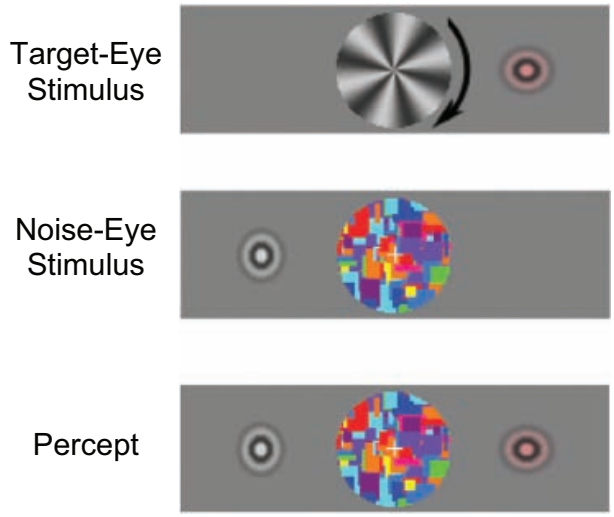


Figure 1.33: Paradigm used by Zhang et al. (2012) to show effects of attentional cueing on CFS. A cue was presented to one side (right in this example) of the target stimulus in one eye and another cue was presented to the other side (left) of the suppressing noise in the other eye. When suppression was measured, the participant was instructed to attend to either the right (in the target eye) or the left cue (in the noise eye), while the eye-of-origin was unknown to the participant. Adapted from Zhang et al. (2012).

A prominent view of how attention modulates relative eye dominance during BR proposes that it influences the effective contrast of an eye's image (Paffen & Alais, 2011). There is evidence of elevated perceived contrast when attention was directed to a stimulus (Carrasco, Ling, and Read, 2004; also see Cameron, Tai, and Carrasco, 2002). Specifically, a spatial cue presented in close temporal proximity to a stimulus increased the apparent contrast of this stimulus relative to an uncued stimulus, and this facilitation effect was absent when the cue and the stimulus presentations were separated by a sufficiently long temporal interval (Figure 1.34). The altered subjective experience induced by attention raises the possibility that visual processing of an attended stimulus is strengthened (i.e. increased neuronal response). Indeed, the enhancement of sensitivity by attention has been well documented (Bashinski & Bacharach, 1980; Carrasco, Penpeci-Talgar,

& Eckstein, 2000; Downing, 1988; Handy, Kingstone, & Mangun, 1996; Hawkins et al., 1990; D. K. Lee, Itti, Koch, & Braun, 1999; Müller & Humphreys, 1991), and has also been shown (in human observers and monkeys) to be correlated with an increased neuronal response, or increased inhibition which leads to a reduction in response when the attended features are either not preferred by the recorded neurons, or presented at the surround of the receptive field (Brefczynski & DeYoe, 1999; Carrasco, 2006; Heinze et al., 1994; Ito & Gilbert, 1999; Luck et al., 1994; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Motter, 1993; Mountcastle, Motter, Steinmetz, & Sestokas, 1987; Spitzer, Desimone, & Moran, 1988; Treue & Maunsell, 1996). Crucially, the observed enhancement was specifically a lateral shift in the contrast response function, implying an increase in the contrast gain (i.e. signal enhancement) rather than a response gain which would otherwise predict an increase in the slope (i.e. the same amount of contrast change corresponds to a larger change in response) (Cameron et al., 2002; Carrasco et al., 2004). Furthermore, the observations that attentional facilitation is dependent on contrast (Figure 1.35; Chong & Blake, 2006; Reynolds & Pasternak, 2000) have reinforced the proposal that this process acts through the modulation of contrast gain (Reynolds & Chelazzi, 2004). Similarly, Blaser, Sperling, and Lu (1999) proposed a computational model where attention serves to enhance the salience of an attended feature, through increasing the gain of the signals (Figure 1.36).

When it comes to BR, studies have illustrated that selective attention to a stimulus plays a comparable role to increasing its physical contrast, in that both can boost the relative dominance of a stimulus[14] (Chong &

[14]Notably, Paffen et al. (2006) showed that reduced engagement of attention during BR slowed perceptual alternations, an effect similar to lowering the contrast of both rivalrous stimuli (e.g. Brascamp et al., 2006).

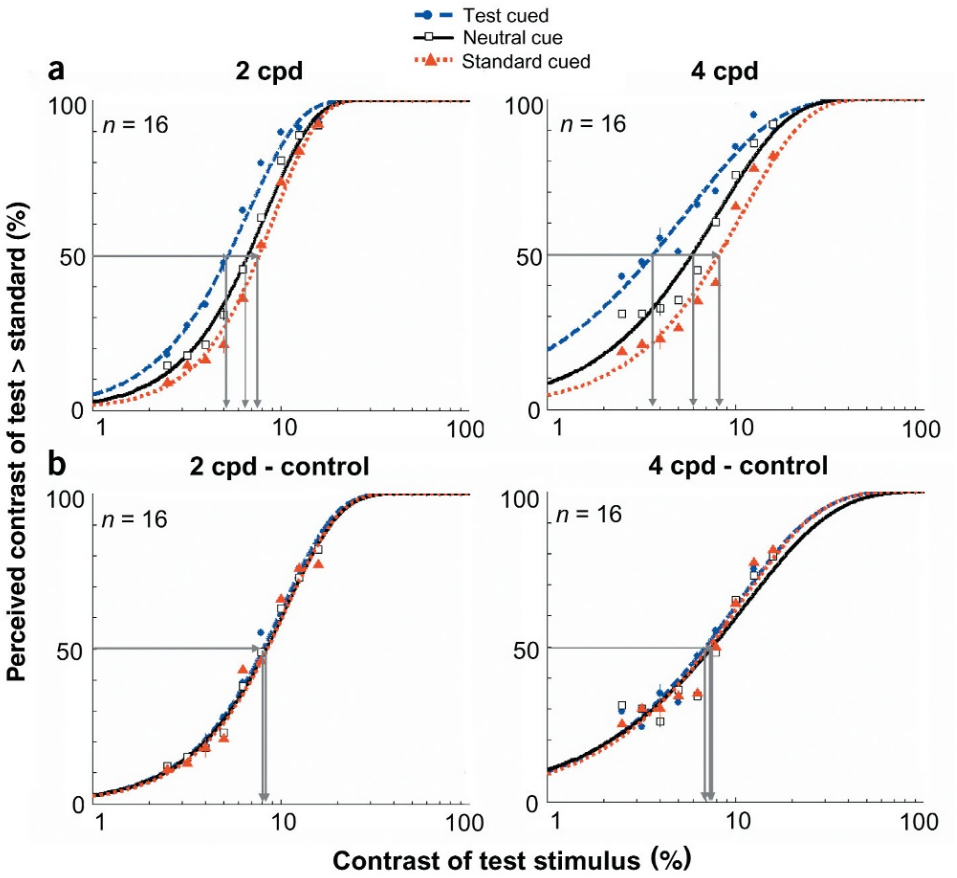


Figure 1.34: Spatial cueing increases apparent contrast. The apparent contrast of a test stimulus increased relative to a standard comparison stimulus when the test stimulus was presented following a cue that appeared at the same spatial location (blue dots). The apparent contrast of the test decreased when the cue appeared at the location of the standard stimulus instead (red triangles). The test was perceived as the same contrast as the standard stimulus when the cue conveyed information of the spatial location of neither stimulus (a neutral cue, black squares). (a) The results for effective cueing when the cue and the stimulus presentations were in close temporal proximity, for two spatial frequencies tested. (b) The results for a control experiment where the cue and the stimulus presentations were separated by a long interval. No cueing effect was found in this case. Adapted from Carrasco et al. (2004).

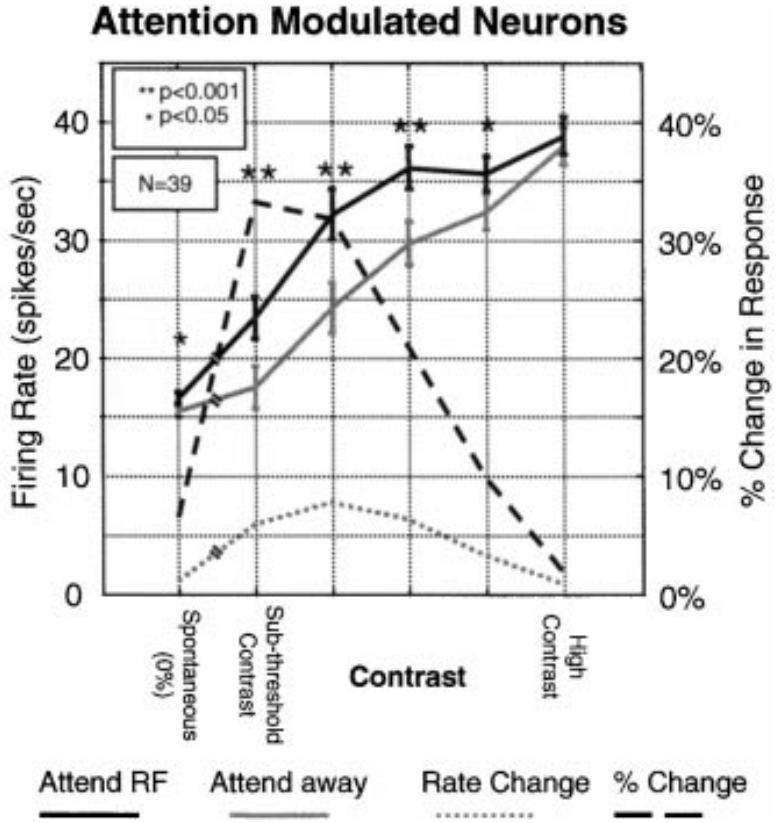


Figure 1.35: Contrast dependence of attentional facilitation. The increase in neuronal responses when attention was directed to a neuron's receptive field relative to the responses when attention was directed away was strongest at intermediate contrast levels of the test stimulus, but it was small at low and high contrast levels. The dotted (left axis) and the dashed lines (right axis) show the absolute and percentage difference in responses between the two conditions, respectively. Adapted from Reynolds and Pasternak (2000).

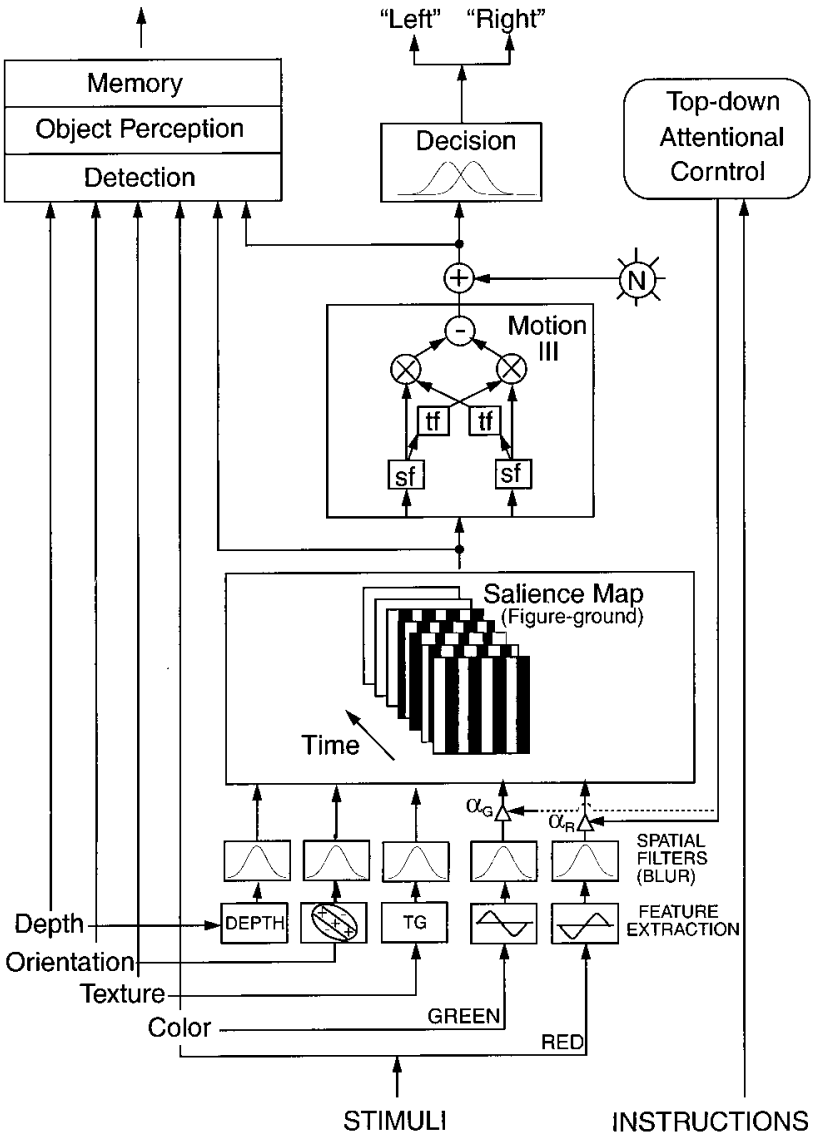


Figure 1.36: A computational model of attentional modulation of perception. Top-down attention increases the signal gain of an attended feature that amplifies the salience of this feature against other unattended features. Adapted from Blaser et al. (1999).

Blake, 2006; Chong et al., 2005). Critically, the increase in dominance due to stimulus selective attention can be counteracted by a reduction in its contrast (Chong & Blake, 2006). This account, though it may not be able to explain all the results regarding the dependence of rivalry dynamics on attention, raises the possibility of a potential bridge between sensory eye dominance and top-down attentional selection.

As proposed in Section 1.11.5, exposure to inter-ocular differences in high-level aspects (e.g. when one eye's image is perceived while the other eye's image is suppressed from awareness) may also alter subsequent eye dominance. It has been shown that exogenously cued selective attention to the non-dominant eye under conditions of BR modifies long-term sensory eye dominance in both typical and amblyopic observers (Ooi, Su, Natale, & He, 2013; J. P. Xu, He, & Ooi, 2010). However it still remains to be seen whether introducing inter-ocular imbalance in endogenous attention is also an effective way to modulate eye dominance.

1.13 Overview

Inhibitory interactions between the two eyes are a key feature of binocular vision, and the balance in terms of inter-ocular inhibition has great relevance to binocular function in both clinically typical and atypical individuals (e.g. Ding et al., 2013a; C. Han et al., 2019; Shooner et al., 2017). This forms a general theme of the present work. This thesis investigates inter-ocular suppression and sensory eye dominance in human vision in eight psychophysical experiments, with a primary focus on BR and CFS.

The starting point of the thesis concerns the relationship between BR and CFS. In Experiment 1, the correlation between individuals' suscepti-

bilities to BR and CFS is explored. The correlation between sensory eye dominance, indexed by the difference in each eye's susceptibility to suppression evoked by these two processes, is also examined. Experiment 2 investigates whether inter-ocular asymmetry in suppression is related to the temporal properties of the stimulus. Experiment 3 looks at the correlation between the degree of eye asymmetry revealed with CFS and the ability to integrate binocular spatiotemporal signals. Experiment 4 seeks to find out whether inter-ocular latency differences can explain the marked individual differences in susceptibility to CFS. Experiment 5 looks at the effect of short-term monocular deprivation on sensory eye dominance measured with BR and CFS. Experiment 6 examines the effects of different variants of monocular deprivation/manipulation on sensory eye dominance. Experiment 7 focuses on the build-up of this effect over time. Experiment 8 looks at the interaction between attentional eye selection and monocular deprivation on sensory eye dominance.

Chapter 2

General methods

Fechner (1860) described an approach to investigating perception, namely psychophysics, which probes the relationship between psychological sensation and the inducing physical stimuli. The present set of experiments reported in this thesis used psychophysical methods to measure inter-ocular suppression and sensory eye dominance. In many of the experiments, an objective forced-choice task was used to quantify the measure of interest. Whenever such a method is used, the sensitivity of each eye can be measured free from any biases related to the response criterion adopted by observers. In addition, the inter-ocular suppression of one eye can be measured independently of the suppression of the other eye[1]. In other cases, subjective perception under conditions of binocular rivalry was measured, whereby the relative contributions from the two eyes were estimated. Although the latter method adopted a subjective measure, it had the benefit that inter-ocular imbalance in the input energy can be avoided (by making the two eyes' stimuli equivalent) which otherwise potentially produces unwanted conse-

[1]This is because under conditions of CFS, the inter-ocular suppression is unilateral, from the dynamic mask in one eye to the static target in the other eye. The suppression of each eye can be measured by manipulating the eye of presentation.

quences on the subsequent eye dominance[2]. This chapter describes the general aspects of the psychophysical methods used in the present work. For specific details that are unique to each experiment, please refer to the methods sections in the experimental chapters.

2.1 Observers

This work examined human binocular vision in the general population (including the author S1), who had normal or corrected-to-normal vision and no history of ocular disease. All the experiments reported were conducted with the approval of the University of Nottingham, School of Psychology Ethics Committee and all participants gave informed consent.

All participants (age range: 21–51 years) had stereopsis (range: 15–120 arcsec) as assessed by the TNO test[3] (Laméris Ootech, Nieuwegein, The Netherlands). For a subset of participants, eye dominance associated with clinical suppression was also measured using the modified Bagolini striated lens test[4] (J. Li et al., 2010). However, preliminary results showed little predictability between this type of measure and the sensory eye dominance measured with the principal protocols used in this work, and hence will not

[2]For example, Kim et al. (2017) have shown that adaptation to conditions of CFS where the eye of presentation was fixed such that one eye was persistently suppressed, for as short as three minutes, induced significant changes in sensory eye dominance.

[3]The participant wore a pair of red-green anaglyph spectacles to detect the orientation of a disparity-defined (cyclopean) object depicted within random-dot stereograms. The smallest disparity at which the judgement could be reliably performed was recorded as a measure of stereoacuity. The results indicated that stereoacuity was in the normal range for all observers tested.

[4]During the modified Bagonili striated lens test, one of the eyes is covered by a neutral-density filter (Wratten; Eastman Kodak, Rochester, NY) while the other eye is uncovered. It measures how much luminance reduction is needed for the filtered eye to induce suppression of the unfiltered eye that breaks binocular combination. The difference in the amount of luminance reduction needed between the two eyes is able to indicate the individual's ocular dominance that is associated with clinical suppression; if one eye is more dominant than the other, the latter requires a greater attenuation in luminance to break binocular combination than does the former.

be formally presented in this report.

As is conventional of typical psychophysical studies, each experiment tested a relatively small number of participants but very extensively, with the exception that a relatively large sample size was employed for Experiments 1 and 3 (Chapter 3). This is because the main purpose of those experiments was to assess the extent and relevance of individual differences and a correlational approach was adopted.

2.2 Apparatus & Stimuli

The stimuli (grey scale except that red/green gratings were used in Experiment 8) were generated using custom software written in C, on an Apple Macintosh, and were displayed on a pair of identical LCD monitors (22 inch Samsung Sync-Master 2233RZ; 1024×768-pixel resolution; 60 Hz refresh rate; 318 cd/m^2 maximum luminance). The utility of using these displays in vision experiments (in terms of spatial, timing and luminance characteristics) has been validated (P. Wang & Nikolic, 2011). The temporal synchronisation of the two monitors was achieved by driving them with the dual outputs of the same video card. They were carefully checked and calibrated with a spot photometer to produce output luminance as a linear function of the digital representation of the image. The noisy-bit method, applied to each colour channel separately, was used to increase the effective number of intensity levels available on each screen (Allard & Faubert, 2008).

For all the experiments reported in this thesis, the stimuli contained conflicting inputs to the two eyes. A Wheatstone mirror stereoscope (Figure 2.1) was employed to enable the dichoptic presentation of the stimuli, which produced an optical viewing distance of 231.5 cm. The angle of the pair of

full-silvered mirrors was nominally ±45° with regard to the median plane of the head, but the angle was adjusted if necessary, for individual observers, to attain stable binocular fusion. On each display stimuli were presented against a uniform "grey" background (159 cd/m^2), within a central square region, enclosed by a high contrast checkered fusion frame (2.21° × 2.21°), with a pair of vertically and horizontally oriented Nonius lines, to assist binocular fusion. A "black" binocular fixation cross was also presented at the centre of the displays between trials in all experiments except for Experiment 4, where the cross stayed on the screens for the whole duration of the task. A chin rest was used to stabilise head position.



Figure 2.1: The mirror stereoscope used to achieve dichoptic presentation—independent images (displayed on separate monitors) could be projected to the corresponding locations in the two eyes, with no cross talk from the stimulus presented to the contralateral eye.

The pair of stimuli used to trigger inter-ocular suppression (CFS or BR)

in Experiments 1–5 (see Section 2.3.1 below) were spatially two-dimensional random noise patterns consisting of square elements ($0.128^\circ \times 0.128^\circ$) presented to one eye, and a horizontally-oriented sinusoidal grating (spatial frequency 1.8 cpd) presented to the other eye (see Figure 2.4). For the noise pattern, the luminance of each element was assigned by random sampling with replacement from a uniform probability distribution spanning a range determined by a Michelson contrast typically of 20% (a contrast of 40% was used in Experiment 4). The grating had a Michelson contrast of 20%, except for Experiment 4 where it was 10%. The phase of the grating was randomly assigned to either $+sine$ or $-sine$ phase on each trial, with respect to the horizontal midline, and each half of the square display window contained an integer number of cycles, preventing luminance artefacts.

For CFS the noise pattern was replaced with a new stochastic sample, usually at a rate of 10 Hz (with the exception that the rate was varied in Experiment 2), forming a dynamic sequence, which served to suppress the grating viewed by the other eye. For BR the pair of stimuli were identical to those used in the CFS task, except that the noise pattern was static rather than dynamic. In addition to measuring the depth of suppression in Experiments 1 and 2, these inducing stimuli for BR were also used for the measurement of subjective perception using a percept tracking task (see Section 2.3.3 below) in Experiment 5.

In Experiments 6–8, a pair of orthogonally-oriented sinusoidal gratings (spatial frequency 1.8 cpd) were used to produce the conditions of BR instead, such that the two eyes had balanced inputs. A vertical grating was presented to one eye and a horizontal grating was presented to the other eye. The phase of each grating was randomly determined to be either $+sine$ or $-sine$ phase on each trial, with respect to the horizontal or vertical mid-

line. In Experiment 8, one eye's grating was red and the other eye's was green, but the stimuli were grey scale in all other experiments (see Figure 2.2). The Michelson contrast of the gratings was either fixed at 20% when temporal dynamics were recorded in Experiments 6 and 7, or varied for measuring psychometric functions with the method of constant stimuli in Experiment 8 as explained as follows. Specifically, the relative contrast (e.g. $(C_{RE} - C_{LE})/(C_{RE} + C_{LE})$ for the right eye's grating[5]) of the gratings viewed by the two eyes was varied from -1 to 1 in seven equal steps. The manipulation of the relative inter-ocular contrast difference was achieved by varying the Michelson contrast of each of the gratings from 0 to 40% in a "see-saw" manner (yielding seven combinations), while the average contrast between the two eyes (i.e. $(C_{RE} + C_{LE})/2$) was kept constant at 20%.

For the measure of binocular integration with the dichoptic motion task (see Section 2.3.2 below), the inducing stimuli were two horizontally-oriented gratings undergone counterphase flicker (sinusoidally modulated in spatial and temporal dimensions; 20% Michelson contrast; 1.8 cpd spatial frequency), one to each eye. The pair of gratings were both temporally and spatially offset by 90 degrees (Figure 2.3). The luminance intensity profiles (L_1 and L_2) at time t for the two gratings are defined by the following equations, respectively (Carney & Shadlen, 1993):

$$L_1(y,t) = L_0(1 + M \times cos(fy) \times cos(\omega t)), \tag{2.1}$$

$$L_2(y,t) = L_0(1 + M \times sin(fy) \times sin(\omega t)). \tag{2.2}$$

L_0 is the mean luminance, m is the depth of modulation, and f and ω are the

[5] C_{RE} and C_{LE} are the contrasts of the stimuli presented to the right and the left eyes, respectively.

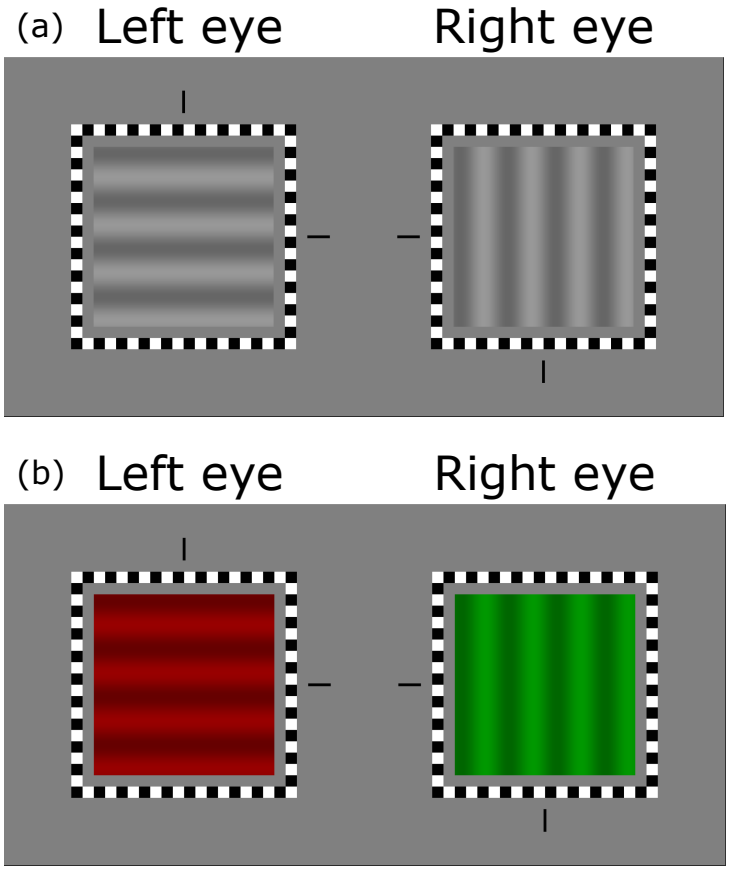


Figure 2.2: A pair of orthogonally-oriented sinusoidal gratings used in some of the experiments to induce the conditions of binocular rivalry. (a) Greyscale gratings used in Experiments 6 and 7 where the Michelson contrast of both gratings was fixed at 20%. The horizontal grating was always presented to the left eye while the right eye viewed the vertical grating. (b) Red and green gratings used in Experiment 8. The colour of the grating presented to each eye was constant within a block of trials, but both colour-eye configurations were tested in different blocks. The orientation-eye configuration was randomly determined on each trial. The inter-ocular difference in contrast was varied across trials by varying the Michelson contrast of both gratings in a "see-saw" manner (see text for details). In this example, both gratings have 20% contrast, giving rise to a relative contrast of 0 for the right eye grating (compared to the left eye grating).

spatial and temporal frequencies, respectively. As the pair of counterphase flickering gratings were presented dichoptically, if perfectly integrated by the visual system in a linear manner, the cyclopean percept is equivalent to the sum of the two gratings, yielding a moving grating defined by the following profile (L_3):

$$L_3(y,t) = L_0(2 + M \times cos(fx - \omega t)). \tag{2.3}$$

The phase of the grating was randomly assigned on each trial, to be –45 or +45 degrees shifted from either $+sine$ or $-sine$ phase with respect to the horizontal midline, with the constraint that the gratings presented to the two eyes were in spatiotemporal quadrature. The direction of the cyclopean motion (upwards or downwards) was also randomly assigned on each trial, which was determined by the direction of phase offest between the two eyes' gratings.

The stimuli were presented in a sequence of frames on the displays. The speed of the cyclopean motion was determined by the temporal phase shift between any two consecutive frames, with larger shifts correspond to faster motion. This phase shift was varied across trials, ranging from 1 to 122 degrees in 12 equal steps.

2.3 Procedure

All experiments were completed in a dimly lit room. The psychophysical tasks used are explained in detail below. Participants practised the tasks extensively before any formal data collection began.

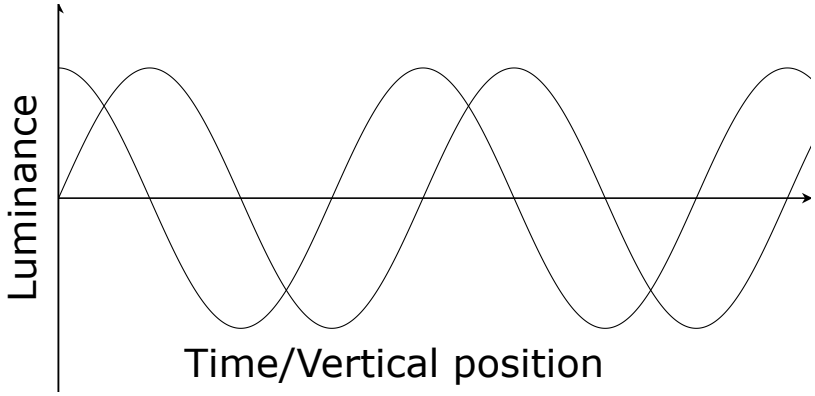


Figure 2.3: Luminance profiles (over time or in vertical position) of the pair of sinusoidal gratings (counterphase flickering) used in the dichoptic motion task. The two gratings were spatially and temporally shifted from each other by 90 degrees.

2.3.1 Measuring inter-ocular suppression using the probe detection task (Experiments 1–5)

A two-alternative forced choice (2-AFC) probe detection task was used to measure the sensitivity of each eye under inter-ocular suppression evoked by CFS or BR (Tsuchiya et al., 2006; see Chapter 1 section 1.5). A typical trial sequence is illustrated in Figure 2.4. At the beginning of each trial the participant was required to view the binocular fixation cross and maintain stable binocular fusion. In Experiment 4 the presentation of stimuli (i.e. a noise pattern to one eye and a grating to the other eye) was initiated by a key press. In Experiments 1–3 where a lower contrast (i.e. 20%) was applied to the noise, the participant waited until the noise pattern completely dominated perception (i.e. it was exclusively perceived), before they pressed a key to initiate the presentation of a test probe. This ensured that the eye viewing the grating was suppressed when the sensitivity of that eye was being measured.

The test probe (i.e. contrast increment) was applied to either the top or bottom half of the grating, chosen at random on each trial. The probe

lasted for 500 ms, with a smooth temporal onset and offset modulated by a Gaussian envelope (SD = 100 ms). A response was expected following the offset of the probe. The dynamic noise for the CFS task was presented for 500 ms and was subsequently removed from the screen in Experiment 4[6], or otherwise it stopped updating following the probe offset and remained on the screen. For the BR task the noise remained stationary. The task was to indicate the probe's spatial location (top vs. bottom). Following a response, the noise and grating were replaced with a uniform "grey" interior (with a fixation cross at the centre) within the fusion frame. The next trial began after an inter-trial interval of 1000 ms.

The contrast increment threshold for each observer was measured using a three-down, one-up adaptive staircase tracking the 79% correct response level, previously described in T. Y. Gao et al. (2018). For the staircase a proportional step size of 30% was used before the fourth reversal and was 15% thereafter. The staircase terminated after 12 reversals and the geometric mean of the last four reversals was used to calculate the threshold for that particular set of trials.

To assess sensory eye dominance revealed with BR and CFS, thresholds were measured with both configurations of eye of presentation. That is, in half the conditions tested, the grating was always presented to the left eye while the noise was viewed by the right eye, and for the remaining trials the converse was true. Baseline increment thresholds were also obtained using an identical procedure, but in the absence of a noise stimulus in the other eye. Participants completed a minimum of five staircases for each condition

[6]In this experiment the effect of the timing relationship between the suppressing dynamic stimulus and the to-be-suppressed target stimulus was investigated. This procedure was therefore to avoid residual influences from the noise which would otherwise occur if it remained on the screen as in the other experiments.

tested[7], in a pseudorandom order and the final threshold for each condition was calculated as the arithmetic mean of these values (the standard error of the mean, SEM, was also calculated).

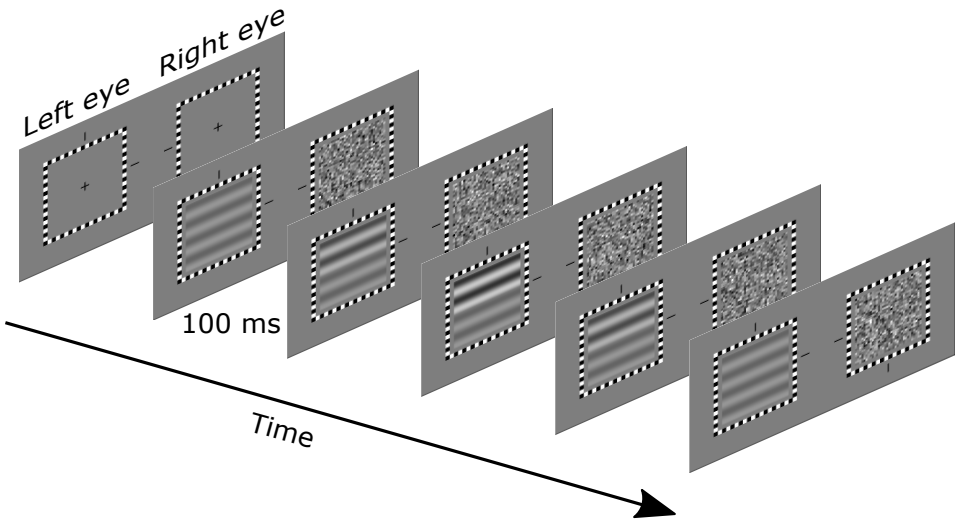


Figure 2.4: Schematic representation of a single trial in the probe detection task (cf. Tsuchiya et al., 2006). After the initiation of the trial, a noise pattern (either dynamic in the case of CFS or static in the case of BR) was presented to one eye (right eye in this example) and a sinusoidal grating was simultaneously presented to the other eye. For CFS the noise image was replaced with a new random sample every 100 ms (i.e. at 10 Hz). A probe (contrast increment) was presented randomly to either the top or bottom half of the grating (top in this diagram), lasting 500 ms and modulated by a Gaussian window with a SD of 100 ms. The location of the probe was judged after its offset.

2.3.2 Measuring binocular integration using a dichoptic motion task (Experiment 3)

A 2-AFC motion direction identification task was used to measure the performance of integrating spatio-temporally disparate binocular inputs. On each trial, the participant maintained stable binocular fixation and initiated the presentation of stimuli by a key press. Each eye's grating gradually flick-

[7]The exception is that S26 completed a minimum of four staircases in Experiment 4.

ered on and off to alter the polarity of contrast over a duration of 500 ms, delivered through a total of 30 frames, each lasting 1/60 s. The participant was required to report the perceived motion direction (upwards vs. downwards) following the offset of the stimuli. This was followed by an inter-trial interval of 1000 ms.

The motion direction judgement performance (percentage of correct responses) was measured using the method of constant stimuli. Each block of testing consisted of 10 trials per phase shift value (12 levels in total; see Section 2.2 above), yielding a total of 120 trials. The order of trials was randomised in a block of testing. Each participant completed at least five blocks of trials in a pseudorandom order[8]. The final performance for a given phase shift condition for each observer was calculated as the percentage of correct responses across all trials. The standard error (SE) of the percentage was also calculated as a measure of inter-trial variability.

2.3.3 Measuring temporal dynamics during sustained binocular rivalry (Experiments 5–7)

The task to measure perceptual dynamics during sustained experience of BR involved a single continuous trial. Following the initiation of a trial, the participant was required to report their perceptual states continuously over the course of the trial by key responses. There were three types of percept to be reported. These included exclusive noise and exclusive grating in Experiment 5, or exclusive horizontal grating and exclusive vertical grating in Experiments 6 and 7. The third response type in all those experiments was mixed percepts of both stimuli. The durations of each type of percept were thereby recorded for subsequent analyses.

[8]The exception is that S18 completed a minimum of four blocks.

In Experiment 5, a trial lasted for a minimum of 60 seconds, whilst it would continue if the last key press was not released at the end of the 60 seconds, to avoid truncation of the last response[9]. In that case the trial terminated upon the key release or once the trial has lasted for 120 seconds. A minimum of five measurements were obtained (for each configuration of eye of presentation). In Experiments 6 and 7, subjective perception during BR was recorded continuously for 3 minutes on each trial, and a minimum of two repetitions were completed. When BR time course was examined in Experiment 6, ten such trials were completed in sequence, with a brief break between trials, yielding 30-minute measurements in each session of testing.

As in the probe detection task, the temporal dynamics of BR was measured with both configurations of eye of presentation in Experiment 5 when the inducing stimuli were a noise pattern and a grating. In Experiments 6 and 7, when a pair of orthogonal gratings were used to induce rivalry, the horizontal grating was always presented to the left eye and the vertical grating was presented to the right eye.

2.3.4 Measuring perceptual dominance at onset binocular rivalry (Experiment 8)

A 2-AFC task was used to measure the perceptual dominance at the onset of BR. At the beginning of each trial the participant was required to view the binocular fixation cross and initiate the presentation of stimuli by a key press. A vertical grating was then presented to one eye for 250 ms and a horizontal grating was presented to the other eye simultaneously. Following

[9]Note that this only applied to responses of exclusive percepts, as it required no key response when a mixed pattern was perceived.

the offset of the gratings, the participant was required to indicate the most dominant, if not exclusive, orientation perceived on that trial. The trial ended once a response has been made, followed by an inter-trial interval of 1500 ms.

Psychometric functions of perceptual eye dominance (percentage response of the dominance of a given eye versus relative contrast of the grating presented to that eye) were obtained using the method of constant stimuli. Each relative contrast level (7 levels in total; see Section 2.2 above) was tested on 20 trials, yielding a total of 140 trials in a block, in which the order of trials was randomised.

The orientation of the grating presented to each eye was randomly selected on each trial. Consequently, the generated psychometric functions were a measure of eye dominance discounting any biases in reported orientation. The colour of the gratings presented to the two eyes was kept constant in a given block of trials (i.e. either green to the left eye and red to the right eye or vice versa), but the data were collapsed across the two configurations. There were at least 2 sets of measurement consisting of 40 responses in total per condition, and the proportion of trials that a left-/right eye dominance was reported formed a data point on a psychometric function for each observer. The standard error (SE) of the percentage was also calculated as a measure of inter-trial variability.

2.4 Curve fitting

The data reported in some of the experiments were fitted with curves. The nonlinear least squares method was chosen for optimising parameter, implemented using the Matlab function *fminsearch*. The details of the fitting

procedures are summarised as follows.

In Experiment 4, the contrast increment threshold as a function of stimulus onset asynchrony (SOA) for each eye of each individual was fitted with a Gaussian-type function with four free parameters (a, b, c, d):

$$y = a \times e^{-(\frac{x-b}{c})^2} + d, \tag{2.4}$$

where y is the threshold, x is the SOA, a is the peak threshold, b is the SOA at the peak, c is the bandwidth (half-width, half-height) of the function, and d is the lowest threshold. For the optimisation of parameters, following constraints were applied: $0 \leq a \leq 90$[10], $c \geq 0$, and $0 \leq d \leq 90$.

In Experiments 5–7, the cumulative density functions (CDF) for the normalised phase durations were fitted with a gamma distribution defined by the following equation:

$$g(x) = \frac{\lambda^\rho}{\Gamma(\rho)} \int_0^x t^{\rho-1} e^{-\lambda t}\, dt, \tag{2.5}$$

where Γ is the gamma function, ρ indicates the shape of the distribution (shape parameter) and λ describes the width (scale parameter). The CDF rather than probability density functions (PDF) was chosen for fitting, to eliminate subjectivity due to introducing an arbitrary bin size.

In experiment 6, the effect of monocular treatment, indexed by the ratio of the treated eye's metric (mean phase duration or predominance) to that of the non-treated eye (for details see Chapter 6), as a function of time since the end of monocular treatment, was fitted with an exponential decay function using the following equation with three free parameters (a, τ, b)

[10]The probe contrast increment threshold could not exceed 90% because the pedestal grating which the probe was superimposed on had a contrast of 10%.

(Lunghi et al., 2013):

$$y = a \times e(\frac{t}{\tau}) + b, \tag{2.6}$$

where y is the computed ratio, t is the time elapsed (in minutes), a is the maximum amplitude, τ is the decay constant, and b is a lower asymptote. For the optimisation of parameters, following constraints were applied: $a > 0$, $\tau < 0$, and $b > 0$.

In Experiment 8, the psychometric functions of perceptual eye dominance in each condition for each individual were fitted with a logistic function with two free parameters (a, b):

$$y = \frac{1}{1 + e^{-a \times (x-b)}} \times 100\%, \tag{2.7}$$

where y is the percentage of responses reporting the dominance of a given eye's stimulus, x is the relative contrast of the stimulus presented to that eye, a reflects the steepness of the curve, and b indicates the relative contrast at which the percentage of either eye's response is 50 (i.e. point of subjective equality, PSE). For the optimisation of parameters, the constraint $-1 \leq b \leq 1$ was applied.

Chapter 3

Individual variation in inter-ocular suppression and sensory eye dominance[1]

3.1 Experiment 1: Individual differences and eye dominance associated with CFS and BR

3.1.1 Introduction

Two representative forms of inter-ocular suppression, namely binocular rivalry (BR) and continuous flash suppression (CFS), revealed important insights on inhibitory interactions between the inputs from the two eyes. An understanding of how these processes operate is fundamentally important not only for explaining binocular vision in the normal visual system, but

[1]Part of this chapter has previously been published as a paper [Wang, McGraw and Ledgeway, 2019b] and in abstract form [Wang, McGraw and Ledgeway, 2019a] and presented at the 41st European Conference on Visual Perception (ECVP, 2018).

also for situations when it is disrupted during development (e.g. Barrett et al., 2004).

Over the last decade or so, our understanding of BR and CFS has advanced significantly, but we still have little understanding of the relationship between these two processes. For example, an important unresolved issue concerns whether CFS is merely an enhanced version of BR (i.e. only quantitatively different), or if they rely on distinct mechanisms (i.e. qualitatively different). This issue has been discussed in light of the past literature in Chapter 1, Section 1.6, but a conclusion could not be reached.

The suppression evoked by CFS and BR are often assumed to reflect the same underlying process and many studies have adopted CFS as an alternative technique to BR to render a stimulus invisible (e.g. Hong & Blake, 2009; Moors et al., 2014; Sterzer, Jalkanen, & Rees, 2009; Yamashiro et al., 2014; Zadbood et al., 2011). However, as substantial methodological differences between studies exist, this necessarily limits the conclusions that can be currently drawn. To rectify this, the present experiment aimed to measure the depth of inter-ocular suppression evoked by both BR and CFS, using directly comparable stimuli and procedures in the same set of participants. As the stimuli used to trigger BR and CFS can be very similar, such that they only differ in terms of the temporal transient energy (Tsuchiya et al., 2006), investigating their relationship may be crucial for understanding the role of temporal properties in the modulation of suppression.

Moreover, inter-individual differences, and variations in sensory eye dominance, are prominent in both the suppression evoked by BR and that under CFS (see Chapter 1, Sections 1.8 and 1.10). These variations provide a useful approach to elucidating the relationship between these two processes. However, the standard practice of pooling data across individuals and eyes,

risks masking substantial variations in binocular vision that exist in the general population. Therefore, another objective of this experiment was to establish the pattern of individual differences in susceptibility to BR and CFS in a representative sample of participants, with normal binocular vision. Potential asymmetries between the eyes with respect to BR and CFS were also assessed, to address the role of sensory eye dominance in inter-ocular suppression.

3.1.2 Methods

Twenty-five subjects participated in Experiment 1 (age range: 21–49 years, 10 females and 15 males). A probe detection task (see Figure 2.4) was used to measure the suppression of each eye, induced by BR or CFS, and monocular contrast increment threshold in the absence of inter-ocular suppression was also measured. Figure 3.1 illustrates the time course of the stimulus contrast profiles on a single trial for the measurements under suppression. For the description of apparatus, stimuli and procedures used in this experiment, see Chapter 2, Sections 2.2 and 2.3.1.

To make sure the stimuli used for BR can legitimately produce typical perceptual alternations, the temporal dynamics were measured using a percept tracking task[2] as a sanity check. Figure 3.2 shows the time course of the percepts experienced by two representative observers. Although individual variations existed in terms of the alternation rate, the data confirmed that these stimuli are valid for inducing normal binocular rivalry.

[2]For procedure see Chapter 2, Section 2.3.3.

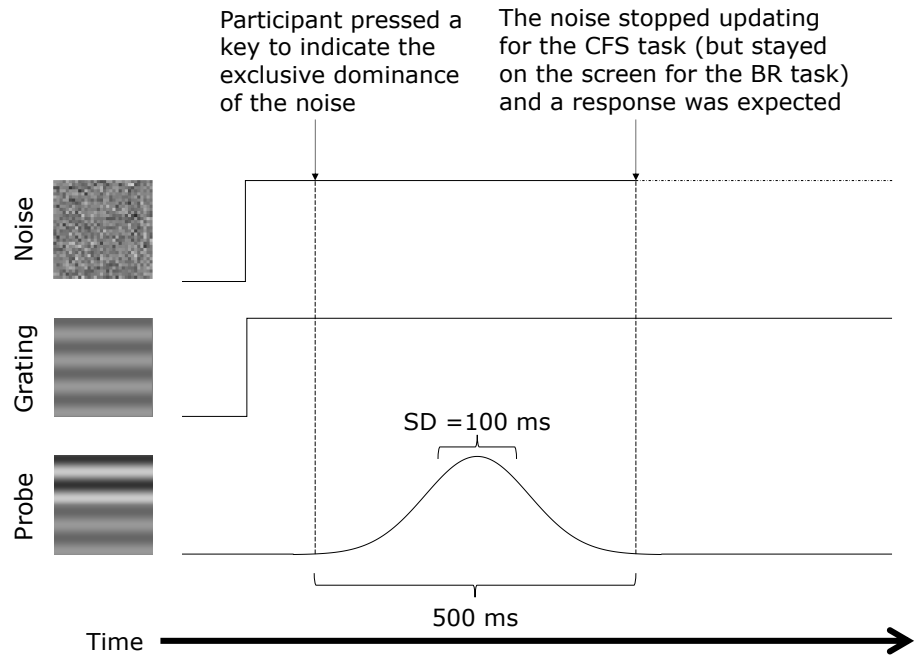


Figure 3.1: The time course of the stimulus presentation (contrast profiles) on a single trial of the probe detection task (see Figure 2.4) used in Experiments 1–3. Once the participant indicated the exclusive dominance of the noise pattern by pressing a key, a probe (contrast increment) was presented randomly to either the top or bottom half of the grating (the top in this diagram), lasting 500 ms and modulated by a Gaussian window with a SD of 100 ms. The location of the probe was judged after its offset.

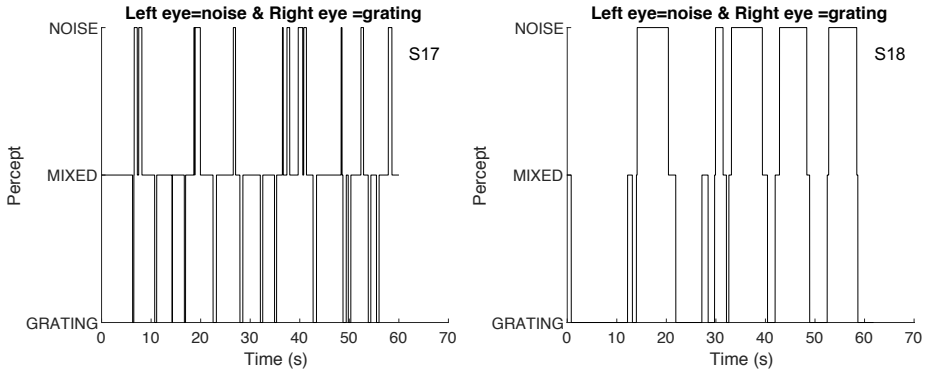


Figure 3.2: Example time courses of percepts during BR on a one-minute trial experienced by two observers (S17 and S18). The ordinate shows the type of percept: exclusive noise, exclusive grating, or mixed percept.

3.1.3 Results

The overall group mean contrast increment thresholds measured under CFS, BR, and the baseline condition (averaged across both eyes, and then across all subjects) are shown in Figure 3.3. These data are plotted in the same manner as Tsuchiya et al. (2006) and despite some differences in the methodologies employed (e.g. the base contrast of the grating; isotropic noise vs. random Mondrians) they exhibited a similar pattern of results, validating the testing protocol used in the current experiment. Both BR and CFS elicited considerable inter-ocular suppression, indicated by the elevated mean probe thresholds compared to that measured in the baseline condition (i.e. monocular increment thresholds). However the depth of suppression elicited by CFS was approximately three times greater.

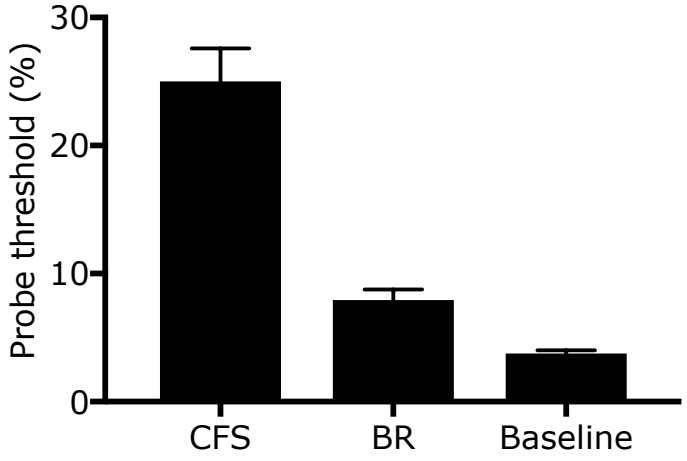


Figure 3.3: Mean contrast increment thresholds (N=25) measured under CFS, BR and in the baseline condition. Error bars represent ±1 SEM across individuals.

To reveal the individual differences within the sample of participants, and also any potential asymmetries between the two eyes with respect to baseline sensitivity, BR and CFS, the right eye's thresholds are plotted against the left eye's thresholds for every observer in Figure 3.4. Consider-

able individual variations in thresholds were evident in all three conditions, whereby the mean increment thresholds, averaged across eyes, ranged from 1.94 to 7.19% for the baseline condition, 2.22 to 20.06% for BR and 5.53 to 53.48% for CFS. That is, there was almost an order of magnitude difference between the lowest and highest thresholds obtained for each condition. The coefficient of variability (ratio of the SD to the mean) shows that the relative variabilities were comparable for thresholds measured under CFS (51.56%) and BR (51.91%), while baseline thresholds were much less variable (35.70%).

Split-half tests were conducted to assess the reliability of the measures of contrast increment thresholds. These were performed by dividing the raw data into two groups (based on whether the position in the order of testing for the run of trials is an odd or even number) and correlation analyses (Pearson correlation coefficient and the Spearman-Brown predicted reliability test) between the two groups of data were carried out. These showed that the odd and even runs of trials were highly, and significantly, correlated in every case: Pearsons r ranged from 0.776 to 0.936; Spearman-Brown r ranged from 0.874 to 0.967. Thus these measurements are reliable to reveal individual performances in this experiment.

In terms of sensory eye dominance in inter-ocular suppression, it is clear from Figure 3.4 that although the thresholds for the two eyes were in general similar (i.e. fall close to a diagonal line with unity slope), for many individuals they were not necessarily the same. To quantify the potential asymmetries between the two eyes with respect to baseline thresholds, BR and CFS, the Spearman rank-order correlation coefficient was calculated for each condition (a non-parametric test was used due to the violation of the assumption of normality assessed by the Shapiro-Wilk test). This showed

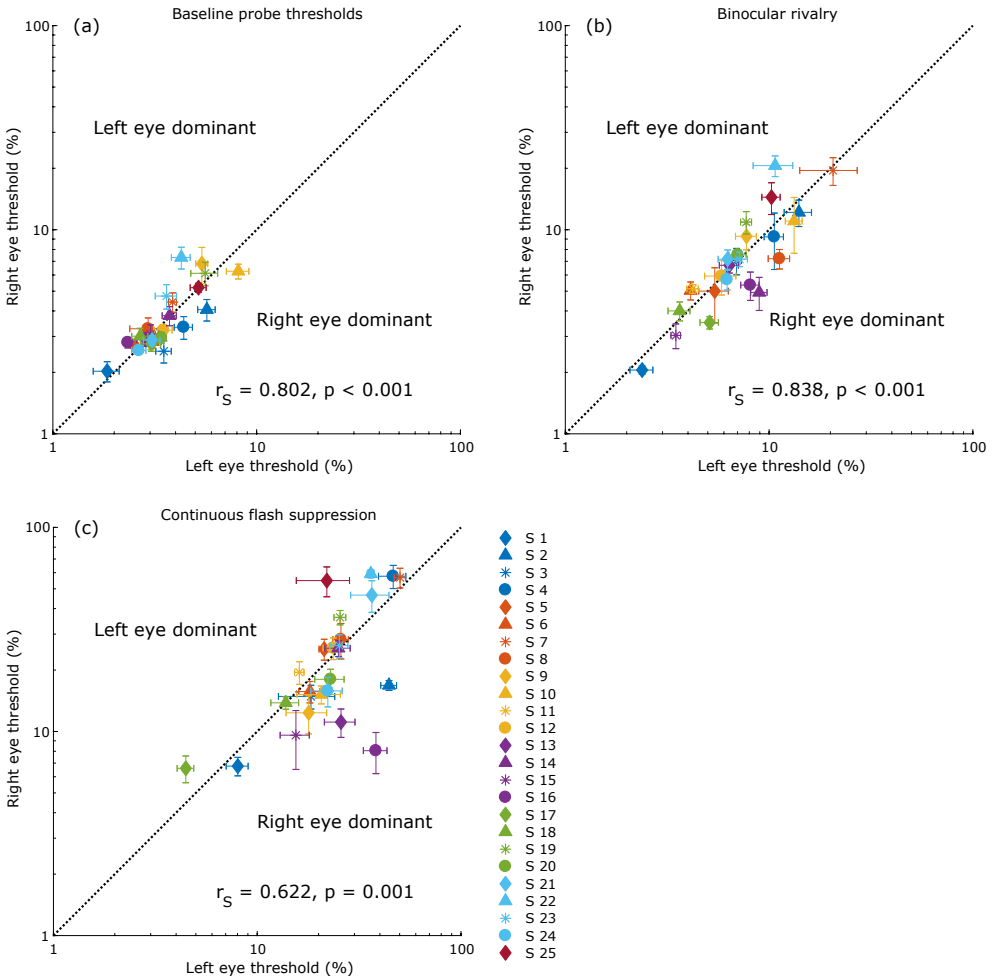


Figure 3.4: Right eye thresholds plotted against left eye thresholds for all twenty-five individuals, measured (a) when there was no suppressing noise (baseline condition), (b) under suppression during BR and (c) under CFS. The diagonal dotted line (of unity slope) on each plot indicates where thresholds would fall if both eyes were equally sensitive to the probe stimulus. Points above the line show higher right eye thresholds than left eye thresholds (left eye dominance), whereas those below the line indicate the converse. Horizontal and vertical error bars represent ±1 SEM calculated across repetitions of the task for each individual. The Spearman rank-order correlation coefficient between the two eyes' thresholds is also shown on each plot.

(see Figure 3.4) that in the sample tested, for all tasks, one eye's threshold was significantly predictable from the other eye's threshold (although r never exceeds 0.84). Nonetheless, inspection of Figure 3.4b and c shows that for BR and CFS tasks there was an overall bias towards right eye dominance in this sample, in that the right eye was less susceptible to suppression than the left eye, and was most evident for CFS.

To investigate the relationship between the degree of suppression evoked by CFS and BR, Spearman rank-order correlations were also conducted between the thresholds measured under the two tasks. To control for the variations in baseline monocular thresholds, partial correlation was used to reveal the relationship between the magnitude of suppression elicited by each task. Figure 3.5 illustrates the residuals of the thresholds measured under CFS versus those for BR, separately for each eye, after partitioning out the variance accounted for by the baseline thresholds. It is evident that performance on the two tasks were significantly associated, although it is worth noting that the correlation for right eye suppression was much weaker than that for the left eye (r of 0.437 vs. 0.729, respectively). This latter result implies that the direction and degree of asymmetric suppression between the two eyes is to some extent task dependent. That is, (as indicated in Figure 3.4b and c) the right eye bias in this sample was much more marked for thresholds measured under CFS than those under BR. Therefore, an additional analysis was conducted to explore the relationship between inter-ocular variations in CFS and BR.

To quantify the eye dominance associated with inter-ocular suppression on each task, a signed asymmetry index was calculated for each participant

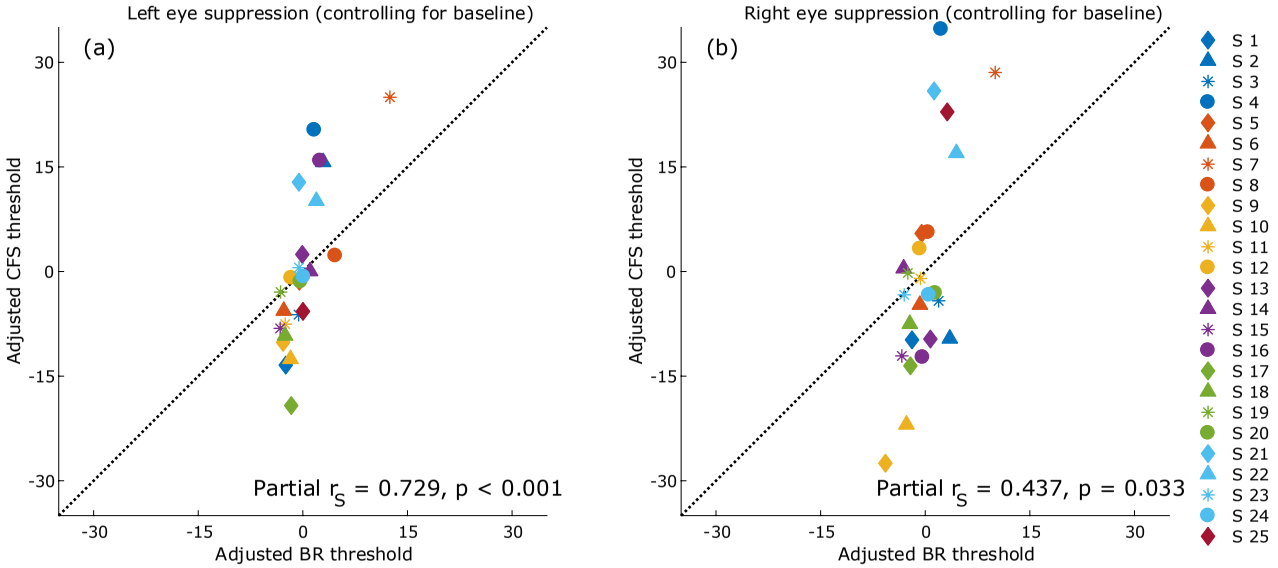


Figure 3.5: Suppression depth measured under CFS versus that measured under BR when the test probe was viewed by the (a) left eye or (b) right eye, for twenty-five subjects. The axes show adjusted thresholds, which are the residuals left after accounting for the variance arising from the monocular baseline thresholds. Note the striking difference between the suppression depth produced by CFS and BR, indicated by the range of the data points on the ordinates and abscissae of identical scales. The results of Spearman partial correlations are shown on each plot. See text for further details.

using the following equation:

$$Asymmetry\,Index = 20 \times log_{10}(\frac{Suppression_{Left\,eye} - Baseline_{Left\,eye}}{Suppression_{Right\,eye} - Baseline_{Right\,eye}}), \tag{3.1}$$

where *Suppression* denotes the mean threshold measured under CFS or BR for the observer, and *Baseline* represents the mean threshold measured in the absence of the noise. This index allows us to directly quantify for each task and observer, the degree of asymmetry between the two eyes' susceptibilities to suppression, whilst discounting any potential baseline differences in monocular increment thresholds. Positive and negative values indicate right and left eye dominance[3], respectively. Whilst zero signifies perfectly balanced suppression between the eyes, higher absolute values of the *Asymmetry Index* suggest a greater degree of bias.

Figure 3.6 plots the asymmetry indices calculated for both BR and CFS (see figure legend). Asymmetric suppression between eyes can be seen in both tasks. One participant (S15) showed no suppression under BR when the grating was presented to her right eye, so it was not possible to compute a meaningful asymmetry index in this case and this participant's data were excluded from further statistical analysis. While many points cluster around zero for both axes (i.e. the centre point) the rest of the points can be found in nearly every quadrant. Spearman rank-order correlations showed that there was no significant association between the indices measured on the two tasks. A Bayes factor was then computed to quantify the evidence for the null hypothesis (i.e. no relationship between the asymmetry indices obtained on the two tasks), based on the method proposed by Wetzels and Wagenmakers (2012). Since the method is designed for parametric

[3]Positive values of the index indicate greater suppression of the test probe when it was viewed by the left eye than the right eye, and therefore indicate right eye dominance.

tests, for the sake of simplicity[4] the data for one other participant (S1, the most extreme outlier) were excluded from this analysis, such that the remaining data became normally distributed. A Bayes factor (BF_{10}) of 0.24 (N=23) was obtained, suggesting substantial to strong evidence for the null hypothesis, according to the categories defined by Jeffreys (1961), that there was no relationship between the asymmetries observed in the CFS and BR tasks.

[4]The results of the Shapiro-Wilk test showed that the asymmetry indices for CFS were normally distributed but this was not the case for BR. Excluding one extreme case, the outlier S1, made the asymmetry indices for BR also normally distributed.

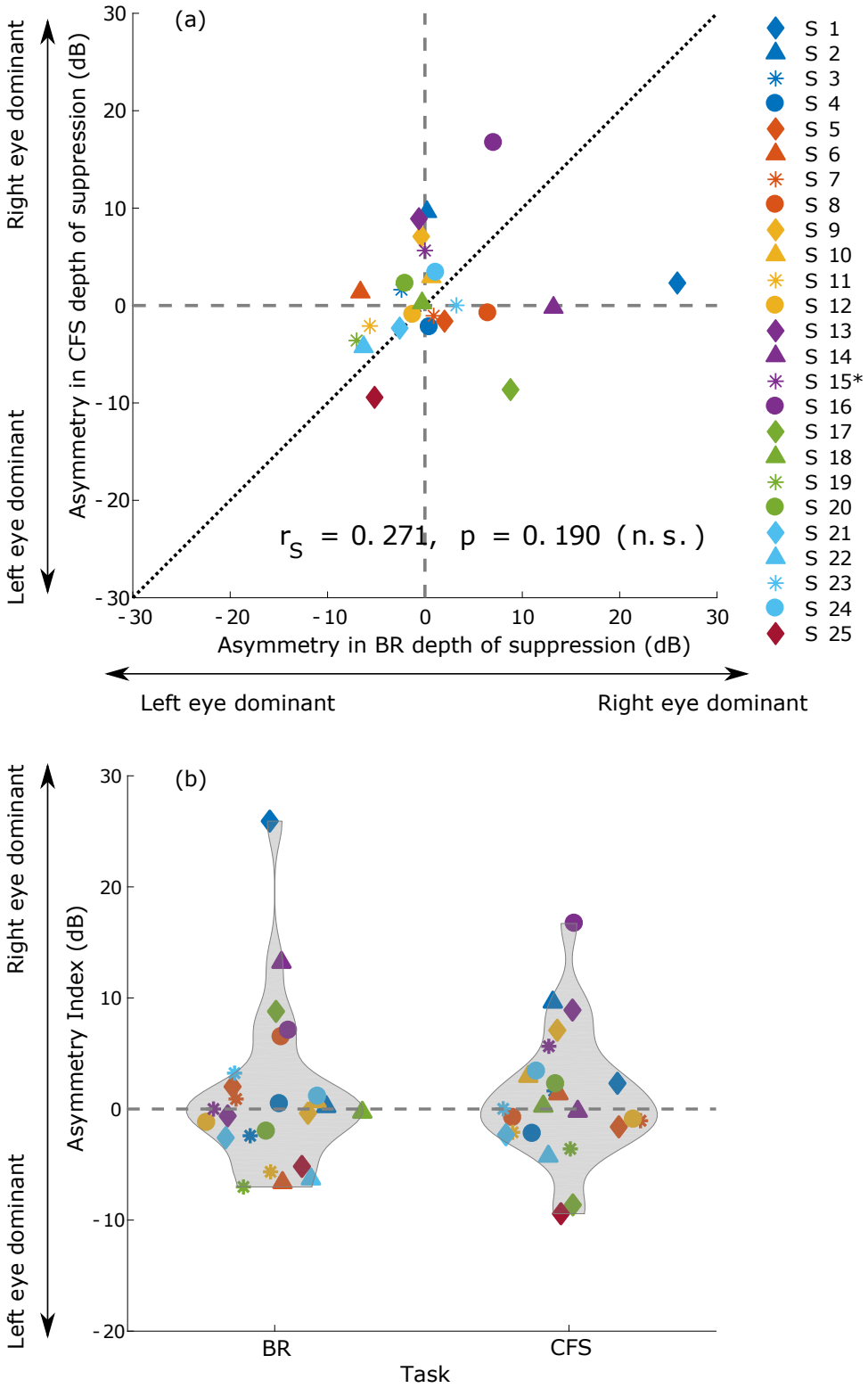

(a)
Right eye dominant
Left eye dominant
Asymmetry in CFS depth of suppression (dB)
30
20
10
0
-10
-20
-30
-30
-20
-10
0
10
20
30
r_S = 0.271, p = 0.190 (n.s.)
Asymmetry in BR depth of suppression (dB)
Left eye dominant
Right eye dominant
S 1
S 2
S 3
S 4
S 5
S 6
S 7
S 8
S 9
S 10
S 11
S 12
S 13
S 14
S 15*
S 16
S 17
S 18
S 19
S 20
S 21
S 22
S 23
S 24
S 25
(b)
Right eye dominant
Left eye dominant
Asymmetry Index (dB)
30
20
10
0
-10
-20
BR
CFS
Task

Figure 3.6 *(previous page)*: The asymmetry indices (Equation 3.1) calculated for the depth of suppression between the two eyes for BR and CFS. (a) The index for every individual is plotted for CFS (ordinate) against that for BR (abscissa). The vertical and horizontal dashed lines indicate symmetric suppression under BR and CFS, respectively. The dotted diagonal line (unity slope) indicates matched asymmetries on the two tasks, in terms of both magnitude and direction. *S15 showed no suppression under BR when the grating was presented to her right eye, so it was not possible to compute a meaningful asymmetry value for this participant and it was therefore conservatively assigned to be zero. The Spearman rank-order correlation coefficient between the indices measured on the two tasks (excluding S15's data) is shown on the plot. (b) The same data are summarised in a violin plot, allowing a direct comparison between the distributions of asymmetry indices for BR and CFS along the same axis.

In summary, profound individual differences were evident in these measures of inter-ocular suppression under both CFS and BR. Whilst the significant correlations between the suppression produced by CFS and BR are at least suggestive of a similar mechanism mediating both phenomena, the finding that sensory eye dominance is task dependent indicates that they might each also engage distinct mechanisms at some stage of binocular processing. This important issue will be explored further in the next experiment.

3.2 Experiment 2: Does the inter-ocular asymmetry in suppression vary with noise refresh rate?

3.2.1 Introduction

The importance of the constantly changing nature of the suppressing stimulus (e.g. dynamic noise) for evoking the potent and robust inter-ocular

suppression found in CFS, compared to other techniques, has been realised since its inception. Tsuchiya et al. (2006), for example, observed that the depth of suppression evoked by CFS depended on the number of updates (i.e. flashes) of a dynamic Mondrian sequence. They found that suppression increased with an increasing number of flashes and reached a maximum with 5 flashes, each separated by 100 ms, equivalent to an image update rate of 10 Hz. A number of later studies have also investigated this issue although there is some variation in what is reported to be the optimal rate that triggers the strongest suppression effect (Shui'er Han et al., 2018; Shui'er Han et al., 2016; Kaunitz et al., 2014; Zhan et al., 2019; Zhu et al., 2016). Nonetheless these findings highlight the crucial role played by transient components in eliciting the relatively high degree of suppression found with CFS compared to BR.

The results of Experiment 1 indicate that even in two tasks both designed to assess the depth of inter-ocular suppression, sensory eye dominance is task dependent. The paradigms used to quantify suppression under CFS and BR differed only in terms of the temporal properties of the noise stimulus: Dynamic noise refreshing at 10 Hz was used to trigger suppression for the former, whilst a stationary noise pattern was used for the latter. This raises the possibility that the differential patterns of sensory eye dominance, observed in the same individuals across the two tasks, may in fact be indicative of differences in low-level temporal properties (i.e. temporal tuning or temporal sensitivity) of the two eyes in response to binocular stimulation. If this is the case, it is reasonable to expect that varying the refresh rate of the dynamic noise pattern in a CFS task will systematically influence the magnitude of any asymmetry observed between the eyes with respect to suppression depth. The aim of the present experiment was to test this

hypothesis.

3.2.2 Methods

Seven representative participants (S1, S2, S4, S7, S8, S13 and S16) who also took part in Experiment 1 participated in this experiment. The apparatus, stimuli and procedure were identical to those used in Experiment 1 with the exception that performance was measured for varying noise refresh rates. Four values of refresh rate were tested—0 (i.e. BR with static noise), 2.5, 5 and 10 Hz. The data reported for thresholds measured in the baseline condition, and with noise refresh rates of 0 Hz and 10 Hz, are those from Experiment 1.

3.2.3 Results

Figure 3.7 shows the contrast increment thresholds for each participant measured as a function of the noise refresh rate. Generally, suppression depth tended to increase as the noise refresh rate was increased, consistent with the findings of Tsuchiya et al. (2006). However participant S1, who showed the least suppression, seemed to exhibit a ceiling effect in that suppression depth appeared to increase little for refresh rates > 2.5 Hz. For observers S2 and S16, although the suppression increased with the noise refresh rate when the test probe was presented to the left eye, thresholds remained relatively constant when the probe was presented to the right eye in all CFS conditions. Nevertheless, when averaged across both eyes, a mixed-effects model analysis incorporating a random effect of individuals, showed a significant fixed effect of the noise refresh rate ($b = 1.97, t_{(26)} = 4.47, p < .001$). Thus despite the discrepancies in thresholds between the two eyes of some

participants, the overall susceptibility to suppression for a given individual increased as the noise rate was increased.

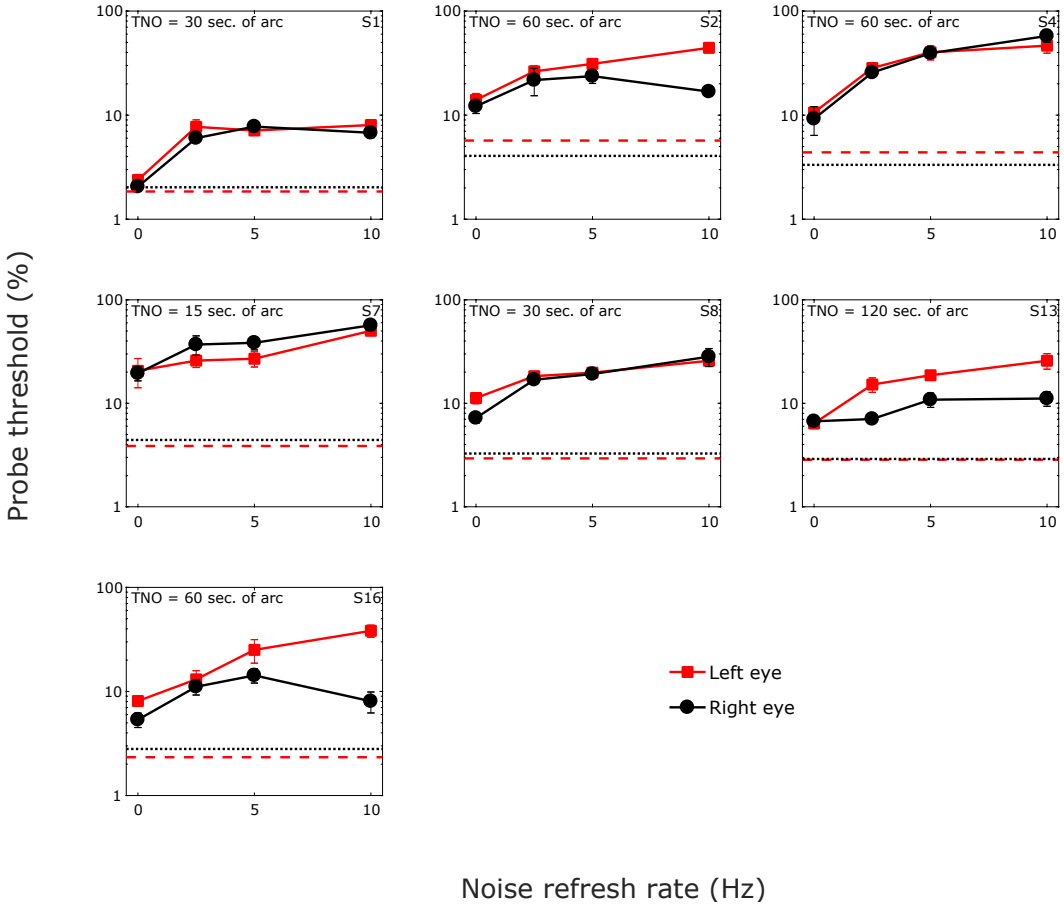


Figure 3.7: Contrast increment thresholds as a function of noise refresh rate. Red squares show thresholds measured when the left eye viewed the test probe while the noise was presented to the right eye. Black circles represent the converse configuration. Red dashed lines and black dotted lines mark the baseline monocular increment thresholds for the left and right eyes, respectively. Error bars represent ±1 SEM calculated across repetitions of the task for each individual. The results of the TNO test (for details see Chapter 2, Section 2.1) for each individual are also shown, as an assessment of the quality of binocular vision.

Despite all participants showing relatively similar baseline monocular increment thresholds for the two eyes, there were some discrepancies in patterns of eye dominance between individuals when the thresholds were measured with a noise stimulus presented to the other eye. First, participants

S1, S4, S7 and S8 exhibited little asymmetry between the two eyes with respect to suppression depth, regardless of the refresh rate of the suppressing noise pattern. In contrast S2, S13 and S16 exhibited marked asymmetries between their eyes, the magnitude of which increased as noise refresh rate was increased. In all cases there was little difference between eyes in the BR condition. These results confirm that asymmetric suppression only exists in some observers, rather than being a universal phenomenon, since not every participant showed different degrees of suppression for the two eyes in one or more conditions. For those observers that did show asymmetric suppression, its magnitude depended strongly on the flicker rate of the noise. Notably, the magnitude of asymmetry was not predictable from the individual's stereo vision (see Figure 3.7 for results of the TNO test).

3.3 Experiment 3: Does eye dominance in inter-ocular suppression predict performance of binocular spatiotemporal integration?

3.3.1 Introduction

The results of Experiments 1 and 2 indicated that there exist individual differences regarding the degree of eye dominance associated with inter-ocular suppression and that these eye asymmetries (if any) tended to increase as the temporal rate was increased. This raises the possibility that the asymmetry (at least in part) lies in the temporal encoding of inputs from the two eyes. If true, not only will inhibitory interactions be asymmetric between

the two eyes, but binocular integration of spatiotemporal signals should also be compromised.

Shadlen and Carney (1986) devised a pair of dichoptic stimuli, producing cyclopean impression of coherent motion, which relies on appropriate integration of the inputs from the two eyes[5]. Specifically, the stimuli comprise two horizontally-oriented gratings, one to each eye, sinusoidally modulated in space and time, which undergo counterphase flicker. The two gratings are offset both spatially and temporally, and if effectively integrated, the observer is expected to perceive a grating moving coherently either upwards or downwards. On the other hand, viewing either grating alone the motion direction cannot be determined, as there is no unified motion direction in either grating. By addressing the display as cyclopean, it means that the motion information can only be extracted when binocular cues are combined.

As this dichoptic motion display entails the processing of temporal information in both eyes, it provides a useful tool to examine whether the difference between the two eyes, in terms of temporal encoding of the input, can account for the noise-rate-dependent asymmetry in inter-ocular suppression in some individuals. Therefore, this experiment investigated the relationship between individuals' perception of dichoptic motion and the eye dominance in terms of susceptibility to CFS.

3.3.2 Methods

A subset of participants (S1–S21, N=21) of Experiment 1 took part in this experiment. The performance of judging the cyclopean motion direction

[5]Linear summation over space and time is required. For details please refer to Chapter 2, Section 2.2.

from a dichoptic pair of gratings in spatiotemporal quadrature was measured using the dichoptic motion task. The apparatus, stimuli and procedure were described in Chapter 2, Sections 2.2 and 2.3.2. Twelve conditions of temporal phase shift were tested for each individual. A wide range of phase shift values were chosen because in pilot testing we found substantial individual differences in terms of the optimal phase shift for perceiving the cyclopean motion. The data for eye dominance revealed with CFS come from Experiment 2, and were reanalysed for the present study.

3.3.3 Results

Figure 3.8 shows the individual performance (percentage of correct responses) on the dichoptic motion task as a function of phase shift for two observers, S1 and S2 who exhibited very different patterns of eye asymmetries measured with the CFS task in Experiment 1 (cf. Figure 3.7). A clear distinction can also be seen between the performance for these two observers on the dichoptic motion task. For S1 (who had little eye asymmetry under CFS), the performance increased dramatically as the phase shift was increased initially, and decreased gradually as the phase shift was further increased. This pattern of results was also the the case for many other participants, although the peak performance varied between individuals. In contrast, S2 (who showed marked asymmetric suppression under CFS) showed chance level performance over the whole range of phase shift tested. In other words, this observer cannot reliably perceive coherent motion from the dichoptic motion display.

To statistically examine the relationship between the ability to integrate binocular spatiotemporal signals and the eye asymmetry revealed with CFS, a correlation test was conducted between individuals' peak performances on

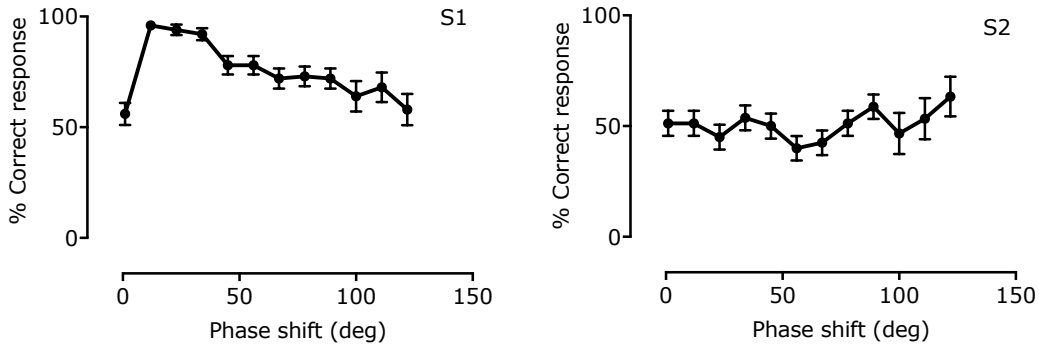


Figure 3.8: Percentage of correct responses as a function of phase shift for two representative observers (S1 and S2). Error bars are ±1 SE of the percentage.

the dichoptic motion task and the absolute values[6] of the asymmetry indices for CFS calculated with Equation 3.1.

Figure 3.9 plots the peak performance (maximum percentage of correct responses) on the dichoptic motion task versus the corresponding individual's asymmetry magnitude on the CFS task. The results of Spearman's test indicated a strong negative relationship between the two measures across subjects. Individuals that elicited rather asymmetric suppression on the CFS task showed difficulty combining binocular inputs to extract motion direction on the dichoptic motion task.

This finding is compatible with the proposal that the asymmetry between eyes observed under CFS may arise from differences in the temporal processing of the inputs from the two eyes. If this is the case, the contributions from the two eyes to (inhibitory or integrative) binocular interactions would differ when there are temporal signals in the input. Both the stimuli used in the CFS task and those in the dichoptic motion task contained temporal signals, and thereby eye asymmetry became measurable.

[6]Thereby they indicate unsigned asymmetries, only showing the magnitude but not the direction.

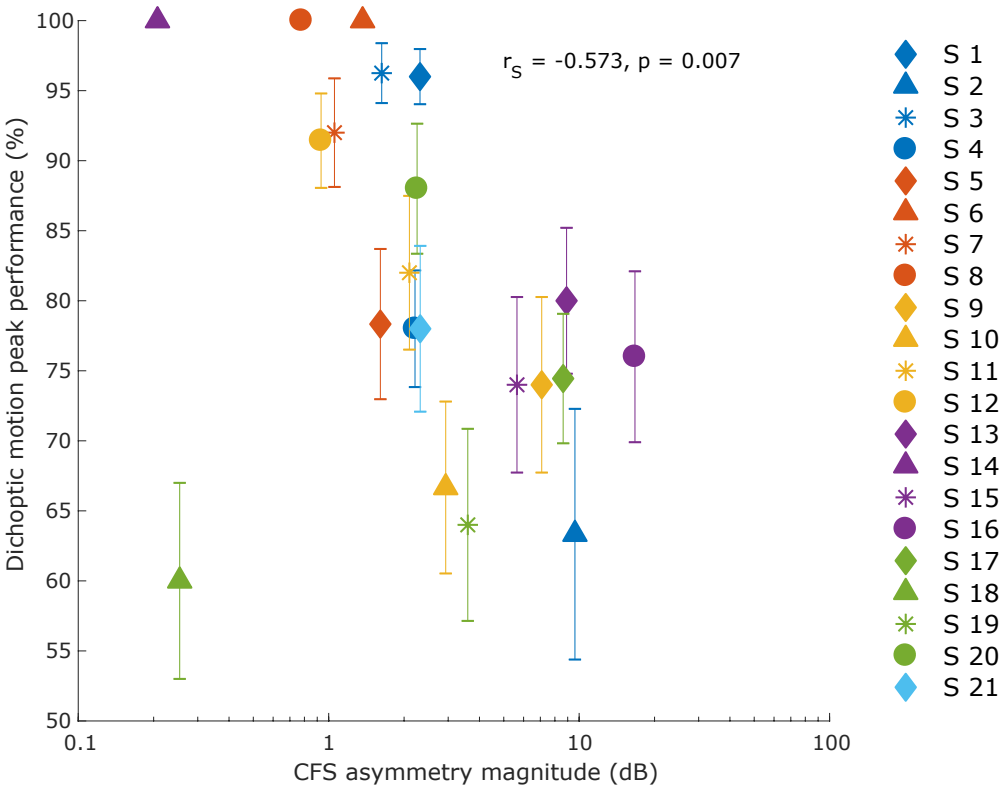


Figure 3.9: Peak performance in percentage of correct responses on the dichoptic motion task versus the magnitude of (unsigned) asymmetry between eyes measured in the CFS task, for twenty-one subjects. Error bars are ±1 SE of the percentage. Results of Spearman's rank-order correlation are also shown.

3.4 General discussion

A common view is that inter-ocular suppression arises when the two eyes are stimulated with incompatible images and that it is mediated by mechanisms that encode binocular differences (see Figure 1.8; Katyal et al., 2016; Katyal et al., 2018; Said & Heeger, 2013). However evidence from modelling studies suggests that inter-ocular suppression might operate under a much broader range of conditions, even when the inputs to the two eyes are identical (e.g. D. H. Baker & Wade, 2017; Meese et al., 2006). Therefore exactly what instantiates inter-ocular suppression is not yet firmly established, but the present thesis focused on perceptual suppression where one eye's image is not consciously perceived due to the presence of a dissimilar image viewed by the other eye. CFS and BR are two representative examples but their precise relationship remains unclear. The results of Experiment 1 revealed significant correlations between the suppression measured in the two tasks, for both directions of inter-ocular suppression (i.e. from left eye to right eye and vice versa). This suggests that a common underlying mechanism is likely to be responsible, at least in part, for evoking the inter-ocular suppression under CFS and BR. Similarly, D. H. Baker and Graf (2009b) reported that a greater depth of suppression under dichoptic masking was associated with longer phase durations during BR. In addition, BR elicited comparable patterns of suppression to those evoked by another type of inter-ocular suppression termed permanent suppression—in both cases the suppression was selective to wavelength, and colour system was affected to a greater extent than luminance system (see Figure 1.19; Ooi & Loop, 1994). These findings collectively suggest considerable overlap in these inter-ocular suppression phenomena.

One of the aims of this study was to address the role of sensory eye dominance in inter-ocular suppression, by assessing potential asymmetries between the eyes with respect to BR and CFS. Sensory eye dominance has previously been reported on a variety of binocular tasks including BR and CFS (e.g. Bossi, Hamm, Dahlmann-Noor, & Dakin, 2018; Dieter et al., 2017a; E. Yang, Blake, & McDonald, 2010). Utilising an objective measure of suppression, it has also been found in the present study that the thresholds measured in the BR and CFS tasks exhibited notable variation (asymmetry) between many of the participants' eyes. Interestingly when an asymmetry index was computed, to quantify the sign and magnitude of each participant's eye dominance on each task, whilst discounting baseline differences in monocular thresholds, there was no significant association between the indices measured on the two tasks. Indeed for half of the participants for which a meaningful asymmetry index could be computed, the sign of the index was different for BR and CFS. That is, for one task a participant's right eye was dominant (less susceptible to inter-ocular suppression) and for the other task the left eye was dominant. This finding could be important in the sense that it might imply some degree of task-dependence for sensory eye dominance. This clearly suggests that although CFS and BR may share one, or more, stages of visual processing, they are not necessarily one and the same (cf. Holopigian, 1989). However, those that showed changes in sensory eye dominance between the two tasks had considerably smaller absolute asymmetry indices (mean = 3.68 $\pm$ 1.20 for BR and 3.00 $\pm$ 0.93 for CFS) than those that did not switch (mean = 5.52 $\pm$ 1.99 for BR and 4.80 $\pm$ 1.38 for CFS). Thus the change in sign is likely to be a noisy result[7]

[7]That said, the results of the Bayes factor still supported the null hypothesis that the signed asymmetry measured under CFS for an individual did not predict that measured under BR, which could be due in part to uncorrelated magnitudes of asymmetry in the

and is consistent with some previous reports on eye dominance (e.g. J. Li et al., 2010).

Whilst the data showed that the range of the asymmetry index values was somewhat wider in BR than in CFS (see Figure 3.6), this may be due in part to the way the index was calculated. That is, it used four measurements (see Equation 3.1) to obtain the final value and the error terms were not taken into account. Consequently errors in the individual threshold values measured would have a multiplicative impact on the final ratio that was computed. With relatively small values in particular, as typically found in the case of BR, the errors may have yielded spuriously large asymmetry scores. This is likely to be the case for some of the observers, such as S1[8]. Consequently further research is needed to address the reliability of this finding.

Phenomenally CFS appears distinct from BR, in terms of the persistent unilateral inter-ocular suppression compared to the stochastic perceptual alternations that are characteristic of BR. However, the stimuli triggering the two processes in the present series of experiments, only differed in terms of the presence or absence of transient components in the noise used for CFS and BR, respectively. It is therefore possible that CFS is just an extreme, but more stable, version of binocular rivalry such that the switches of perceptual dominance are minimised by the temporal characteristics of the noise. Commensurate with this suggestion, there is evidence that neural adaptation may be the mechanism underpinning perceptual alternations in BR (see Chapter 1, Section 1.7; Alais, 2012; Alais et al., 2010; Kang & Blake, 2010; Laing & Chow, 2002; Lankheet, 2006; Shimaoka & Kaneko,

two cases.

[8]The range of individual asymmetry indices revealed with BR becomes narrower than that with CFS if excluding this subject's data (see Figure 3.6b).

2011; H. R. Wilson, 2003). If this is the case, the transient nature of the suppressing stimulus (e.g. dynamic noise) used to evoke CFS might serve to preclude or reduce adaptation of the mechanism encoding the noise, compared with the mechanism encoding the persistent static image presented to the other eye, such that it can dominate perception for a relatively prolonged period of time.

It was found in Experiment 2 that the depth of suppression increased when the noise was updated at a faster rate, up to a value that is conventionally used (10 Hz) in experiments employing a CFS task (Tsuchiya & Koch, 2005; Tsuchiya et al., 2006; E. Yang & Blake, 2012). Although the optimal refresh rate to trigger inter-ocular suppression is still under debate (Shui'er Han et al., 2018; Shui'er Han et al., 2016; Kaunitz et al., 2014; Zhan et al., 2019; Zhu et al., 2016), the present finding that the depth of suppression systematically varied with flicker rate, underscores the crucial role of temporal transient energy in the modulation of suppression evoked by CFS.

Importantly, the results revealed that asymmetric inter-ocular suppression, present in a subset of our participants, whilst modest in the case of BR, increased when the noise was flashed and as its rate was increased. This finding suggests that the asymmetry may arise from the difference in the temporal encoding of the two eyes' signals. This proposal has been strengthened by the results of Experiment 3 where binocular integration of spatiotemporal signals was compromised in individuals who showed evident asymmetric inter-ocular suppression under CFS. Moreover, a likely source of the temporal-rate-dependent asymmetry is the presence of multiplicative noise in the non-dominant eye's channel. This is because depth of suppression under CFS critically depends on the spatiotemporal relationship

between the mask and the target stimuli (Tsuchiya et al., 2006), and introducing multiplicative noise in the eye viewing the mask would therefore weaken the suppression elicited, by interfering with the analysis of the spatiotemporal information of the mask stimulus. The choice of multiplicative rather than additive noise is on the basis that the temporal structure of the mask stimulus modulates depth of suppression. In that sense, applying multiplicative noise in one eye would make the amount of reduction in inter-ocular suppression elicited by that eye relative to the suppression in the opposite direction vary as noise rate is varied, which is indeed the pattern of results found in the present experiment. Curiously, multiplicative noise has also been applied in psychophysical and modelling studies to account for the asymmetric processing found in amblyopia (D. H. Baker, Meese, & Hess, 2008; Levi & Klein, 2003; Levi, Klein, & Chen, 2007). This resemblance raised the possibility that the eye asymmetries present in the laboratory-induced inter-ocular suppression in normal observers may simply differ quantitatively, but not qualitatively, from those in amblyopia.

Furthermore, that the lack of obvious asymmetry in the thresholds measured in the baseline condition, implies that monocular thresholds cannot be the origin of the asymmetry in thresholds measured under suppression. Instead, the asymmetry occurs at a stage where the inputs from both eyes interact. Consistent with this finding, C. Han et al. (2018) have shown that the imbalance in sensory eye dominance cannot be fully accounted for by a discrepancy in monocular contrast thresholds and that at least some degree of the asymmetry must be purely binocular.

The seemingly contradictory conclusion, that a common mechanism might underpin CFS and BR whilst they differ in terms of sensory eye dominance, may be reconciled in the following sense. These results are in line

with the suggestion that the differential patterns of sensory eye dominance, observed in some individuals across BR and CFS tasks, arise due to differences in the temporal response properties of the two eyes under conditions of inter-ocular suppression. This suggests that the nature of the inter-ocular suppression underlying the two processes is likely to be the same, but the introduction of temporal transient energy in the stimulus viewed by one eye in CFS may reveal intrinsic differences between the eyes, in some individuals (even with normal binocular vision), associated with the visual processing of those components.

It is tempting to speculate that clinical suppression, typically found in strabismus and amblyopia, is mediated by the same mechanism as laboratory-induced suppression (e.g. BR). Some research has provided evidence that the suppression in amblyopia exhibits a similar time course to rivalry suppression (Wolfe, 1986). Where their time courses differ, they can be equated, in amblyopia and normal subjects, using neutral density filters (Leonards & Sireteanu, 1993). However, strabismic suppression is not tuned to wavelength as is typically the case in BR (Ooi & Loop, 1994; Smith III et al., 1982; Smith III et al., 1985). This finding may provide a useful insight for future investigations into the relationship between laboratory-induced inter-ocular suppression, and clinical suppression that is pathologically present in atypical visual development.

In summary, individual differences in suppression depth measured using CFS are likely to be commonplace in the general population, and are predictive of performance on an analogous BR task. However sensory eye dominance is task dependent and can be different for BR and CFS in the same individual. This latter finding may have important practical implications, when using tests of inter-ocular suppression to assess eye dominance,

both in the general population and in clinical cases. It has also been demonstrated that asymmetries in suppression for the two eyes depend critically and systematically on the temporal properties (flicker rate) of the noise stimulus inducing that suppression. A possible explanation is that differences in temporal processing arising between the two eyes, under conditions of sensory conflict, can lead to marked asymmetries in the efficacy of inter-ocular suppression, forming an important area for further research.

Chapter 4

Experiment 4: Can inter-ocular latency differences explain individual variation in CFS?

4.1 Introduction

In Chapter 3, marked inter-individual variations can be seen in terms of the susceptibility to CFS from the results of all three of the experiments. The importance of inter-ocular latency difference in binocular vision has been stressed earlier in Chapter 1, Section 1.9, which raises the possibility that individual variations in this latency difference may explain the differences in CFS between people.

An illustration of this hypothesis is shown in Figure 4.1. Suppose that the red and the black curves represent the modulation of suppression under CFS by the stimulus onset asynchrony (SOA) between the suppressing

stimulus and the target exhibited by two hypothetical observers. The lack of strong suppression at zero SOA (the dotted line) as shown by the black curve might be due to the lateral shift of the modulation function to the right relative to that of the red curve. That is to say, this observer may still have the potential to elicit suppression as strong as that shown by the red curve, but the depth of suppression is not optimal at zero SOA; this results from a latency difference between the propagation of information by the two eyes, such that the two stimuli do not simultaneously reach the stage at which binocular information is combined. If this is true, we are able to conclude that the individual differences in the measured depth of suppression under CFS are not variability in susceptibility to CFS *per se*, but instead, these are the consequence of variability in temporal processing arising from inter-ocular delay. Furthermore, this hypothesis also predicts a horizontal displacement of the suppression function of SOA for an individual's two eyes, if low suppression at zero SOA is due to an inter-ocular latency difference.

Tsuchiya et al. (2006) have provisionally explored the dependence of depth of suppression on the SOA between the suppressing stimulus and the target (Figure 4.2), but crucially they averaged data both between eyes and across individuals, which would have masked any impact of variations in inter-ocular latency difference on inter-individual variability in depth of suppression. We therefore set out to examine the aforementioned hypothesis by the following experiment.

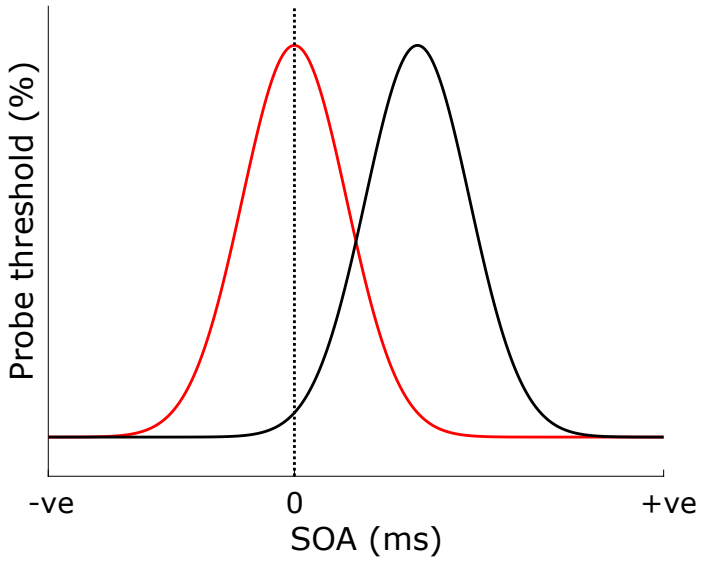


Figure 4.1: The hypothetical pattern of CFS suppression as a function of stimulus onset asynchrony (SOA) between the suppressing stimulus and the target probe. It could be the horizontal shift of this function that results in the marked variations in depth of suppression (indicated by probe threshold) among individuals. When the SOA is zero (indicated by the vertical dotted line), whereby the onset of both stimuli coincides, the suppression for one subject (red curve) is much higher than that produced by the other subject (black curve) in this figure. However, the maximum suppression for the latter could be as high as the first subject but only when measured at a longer SOA (sign of which depends on which of the two eyes' images has the longest latency).

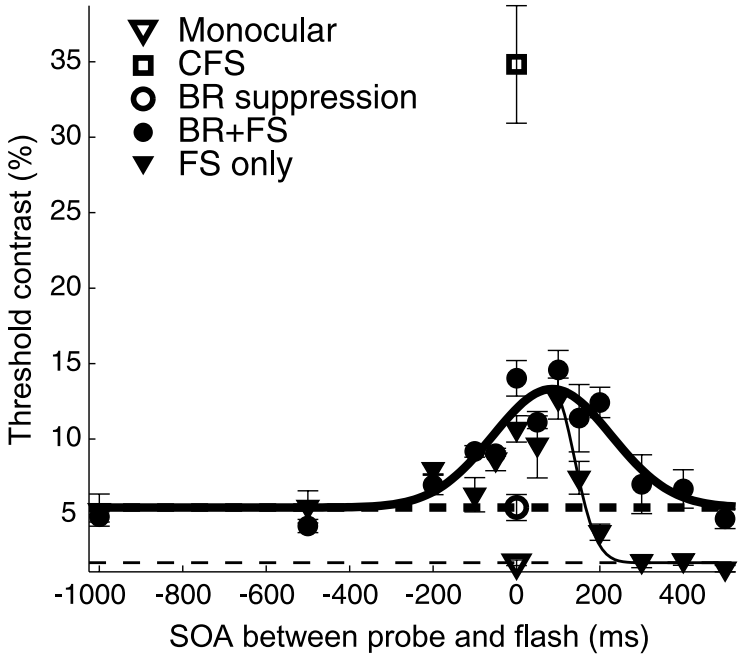


Figure 4.2: SOA dependence of inter-ocular suppression shown by Tsuchiya et al. (2006). The probe thresholds were measured under conditions of flash suppression (FS only) or a modified version (BR+FS). In the FS condition, a grating was presented to one eye, and the other eye viewed a blank field, followed by a Mondrian pattern (the suppressing stimulus) which had a transient onset, forming a single "flash". In the BR+FS condition, the presentation of the Mondrian pattern and the grating occurred simultaneously. In both conditions, the SOA between the Mondrian pattern and the test probe was varied. The data shown in this figure were averaged between the two eyes and across four observers, and indicated a peak suppression when the probe was presented approximately 100 ms before the Mondrian pattern appeared.

4.2 Methods

Five subjects took part in this experiment[1]. The CFS protocol was described in Chapter 2, Section 2.3.1. Contrast increment thresholds for reliable judgement of the probe location were measured to estimate depth of suppression (see Figure 2.4). Figure 4.3 illustrates the timing relationship between stimulus presentations. The pedestal grating was presented to one eye as soon as a key was pressed by the participant to indicate the beginning of a trial. The test probe was presented to the same eye 500 ms later. The SOA between the dynamic noise and the probe was varied across 13 conditions (except that S26 completed 12 conditions), ranging from -400 to 400 ms. This was achieved by varying the onset of the noise. For SOAs < 0, the noise onset preceded the probe onset, whereas for SOAs > 0 the converse was the case. Baseline monocular thresholds for each eye, in the absence of the dynamic noise pattern in the other eye, were also measured.

4.3 Results & Discussion

The probe thresholds (contrast increment) for the left eye (red) and right eye (black) of each observer, as a function of the SOA between the noise pattern and the test probe are shown in Figure 4.4. The data for each observer are well characterised by Equation 2.4 and the estimated parameters and goodness of fit are summarised in Table 4.1[2].

[1]These included S1 who also participated in Experiments 1–3, and four other new subjects.

[2]The degrees of freedom reported in the table were calculated by subtracting the number of free parameters of the fitted curve from the number of data points used. Only 12 conditions were tested for S26 compared to 13 conditions for other participants, leading to different degrees of freedom.

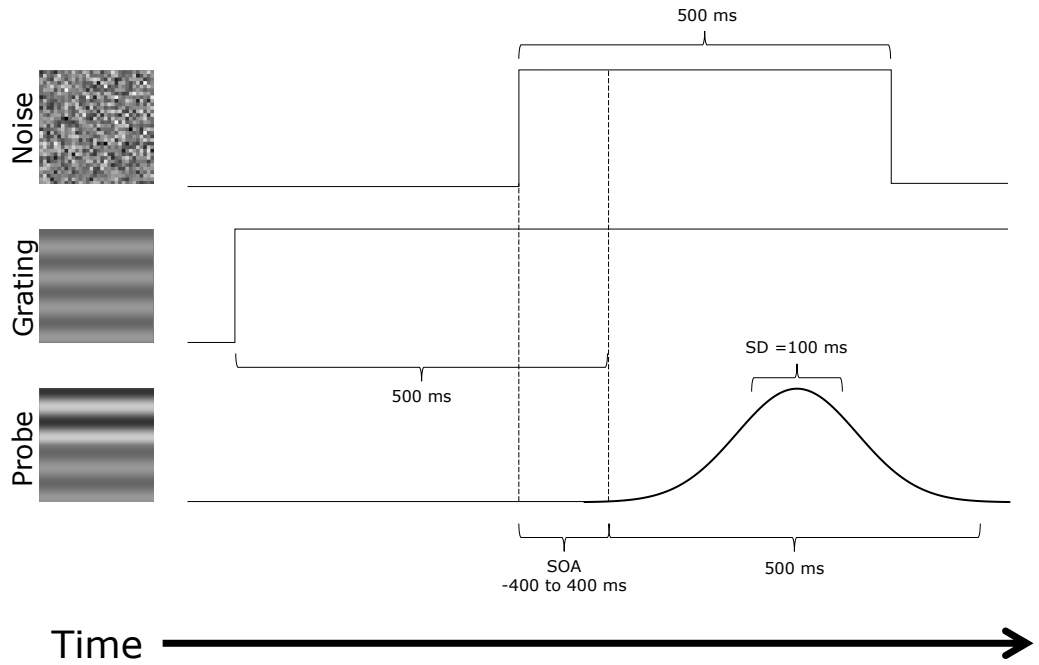


Figure 4.3: The time course of the stimulus presentation (contrast profiles) on a single trial in Experiment 4. The presentation of the pedestal grating was initiated by a key press and stayed on the screen until the end of the trial (middle panel). The test probe (i.e. contrast increment applied to either the top or the bottom half of the grating), whose onset and offset were smoothed by a Gaussian window with a SD of 100 ms, was presented 500 ms following the onset of the pedestal grating, for a duration of 500 ms (bottom panel). The noise pattern was presented for 500 ms, but the onset was varied relative to that of the probe, and this SOA ranged from -400 to 400 ms (top panel).

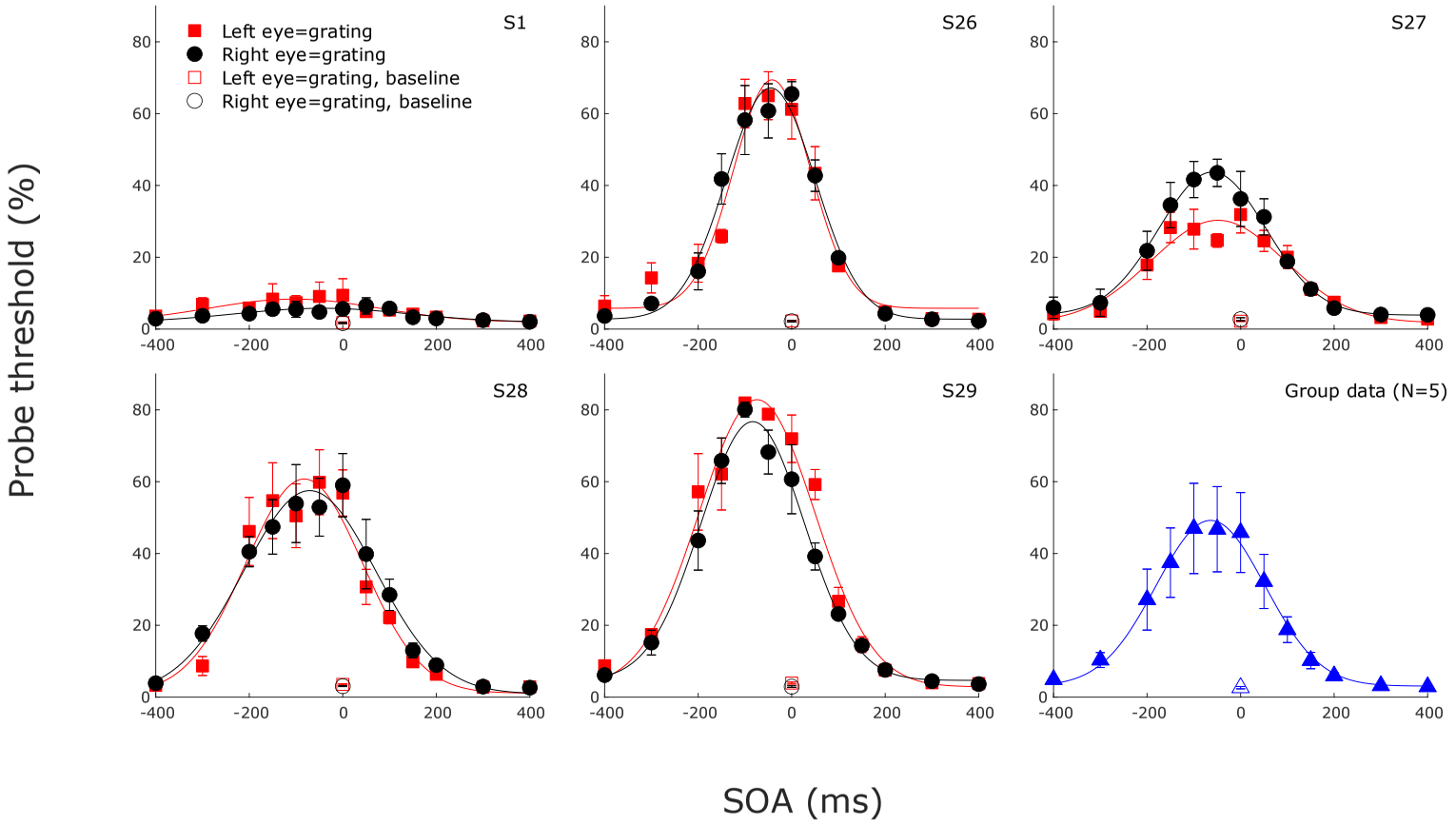


Figure 4.4: Contrast increment thresholds under CFS (noise contrast = 40%), for the left and the right eyes, as a function of the SOA between the noise and the probe for five observers (filled symbols). The curves are fits (Gaussian plus constant; see Equation 2.4) to the data of each eye. Baseline monocular thresholds for each eye of the observers are also shown (open symbols), plotted at zero SOA for illustrative purposes only. The bottom right graph shows the data averaged across eyes and subjects (blue triangles). Error bars represent ±1 SEM (across repetitions for individual data or across subjects for average data).

Table 4.1: The estimated parameters and goodness of fit for a Gaussian-type function (Equation 2.4) fitted to the data for the left and right eyes in Experiment 4. The 95% confidence bounds are shown in brackets.

Observer	a (amplitude-%)	b (SOA at peak-ms)	c (bandwidth-ms)	d (minimum height-%)	R^2	df
			Left eye			
S1	6.44 (3.68, 9.19)	-104 (-157.2, -50.73)	257.9 (117, 398.7)	1.91 (-0.82, 4.65)	0.82	9
S26	63.61 (53.53, 73.68)	-41.97 (-55.36, -28.59)	116.6 (93.31, 139.9)	5.8 (0.11, 11.48)	0.97	8
S27	28.54 (23.1, 33.98)	-48.31(-71.17, -25.44)	202.1 (146.9, 257.2)	1.76 (-3.21, 6.73)	0.95	9
S28	59.64 (50.28, 68.99)	-82.49 (-101.8, -63.19)	176.7 (136.2, 217.2)	1.11 (-6.48, 8.7)	0.96	9
S29	79.96 (71.1, 88.82)	-74.17 (-87.54, -60.81)	175.1 (146.9, 203.3)	2.87 (-4.27, 10.01)	0.98	9
			Right eye			
S1	3.9 (1.86, 5.95)	-43.85 (-95.26, 7.57)	262.7 (83.4, 442.1)	1.88 (-0.3, 4.07)	0.81	9
S26	64.39 (57.43, 71.35)	-44.95 (-55.29, -34.62)	134.4 (115.2, 153.7)	2.77 (-1.58, 7.11)	0.98	8
S27	39.83 (37.39, 42.28)	-60.26 (-67.16, -53.36)	161.7 (147.7, 175.7)	3.89 (2.06, 5.72)	0.99	9
S28	56.59 (49.73, 63.44)	-70.64 (-85.66, -55.61)	199.2 (164.6, 233.8)	0.92 (-5.22, 7.06)	0.98	9
S29	72.05 (67.64, 76.46)	-83.25 (-90.29, -76.2)	156.5 (142.5, 170.5)	4.67 (1.47, 7.87)	0.99	9

In spite of the comparable monocular thresholds (measured in the absence of inter-ocular suppression), clear variations in probe thresholds under CFS can be seen among these participants. These variations were however obscured when the data were averaged across eyes and subjects, as shown in the bottom right graph in Figure 4.4 (cf. Figure 4.2). Specifically, the variations primarily lay in the magnitude of the peak thresholds of the functions obtained for these individuals which indicated the maximum depth of suppression (for the conditions tested), whereas the SOA at the peak was very consistent both across individuals and between eyes. For S1, for example, the probe threshold was universally low in all SOA conditions, and for both eyes. In contrast, subjects like S26 exhibited high thresholds when the SOA was small (the onset of the dynamic noise and that of the probe were in close temporal proximity) and the thresholds decreased as the SOA was increased, which was the case for both eyes. These results are clearly inconsistent with the hypothesis that individual differences in depth of suppression under CFS are simply due to a horizontal displacement, rather than a discrepancy in the amplitude, of the two eyes' thresholds as a function of SOA (cf. Figure 4.1). Moreover, the functions for the two eyes of most subjects appeared to be very similar, and a paired-samples t-test indicated that the eye difference in SOA at the peak was not significant ($t_{(4)} = -.72, p = .51$). A Bayes factor (BF_{10}) of 0.488 was obtained, suggesting some evidence for the null hypothesis (based on the categories defined by Jeffreys (1961)) that the SOA at the peak threshold for the two eyes does not differ. This finding also precluded the possibility that the low suppression at zero SOA found in some individuals are due to marked inter-ocular latency differences. In any cases when there was a difference in thresholds between an individual's two eyes (e.g. S27), it was in terms of the magnitude of the peak threshold,

but not the SOA at which the peak threshold was elicited. This difference in amplitude of the modulation functions revealed an asymmetric susceptibility to CFS between the two eyes, a phenomenon that has been obscured in previous research (e.g. Tsuchiya et al., 2006).

Intriguingly, for all observers, the maximum suppression was elicited when the dynamic noise was presented slightly earlier in time than the probe (i.e. at a small negative SOA; left eye: mean = -70.19, SD = 25.42 ms; right eye: mean = -60.59, SD = 16.88 ms). One-sample t-tests showed that the SOA at the peak threshold was significantly less than zero, for both the left eye ($t_{(4)} = -6.17, p = .003$) and the right eye ($t_{(4)} = -8.03, p = .001$). These results may reveal the time required for inter-ocular suppression to take place. That is, it takes approximately 50 to 100 ms for the neurons excited by the encoding of the dynamic noise, to elicit inhibition on the neurons encoding the target. One possibility is that it may require a minimum number of noise transients (approximately 2) before it could elicit optimal suppression of the target in the other eye.

Alternatively, these results may arise from a discrepancy in the latency of the visual processing of the two stimuli used in this experiment (i.e. stimulus-specific latency difference in contrast to the proposed latency difference between eyes). It is possible that the broadband, dynamic noise, containing transient components, takes somewhat longer time to process, than does the temporally-smoothed sinusoidal probe. If this is the case, the small negative SOA where the peak of the modulation function was obtained, however, may be specific to the stimuli used in this experiment, and it remains unknown whether varying the attributes of stimuli will result in different conclusions about the optimal SOA at which the maximum suppression can be elicited.

Notably in the results of Tsuchiya et al.'s (2006) study (see Figure 4.2), the suppression was strongest when the probe onset proceeded the flash onset by approximately 100 ms, appearing to contradict the findings of the current experiment. Nevertheless, the SOA in that study was in reference to the onset when the suppressing stimulus pattern was replaced with a new random pattern (to form a flash), whereas in the present experiment it was the presentation onset of the suppressing stimulus that was manipulated. In addition, other differences in stimulus attributes, such as the contrast and the pattern of the suppressing stimulus (visual noise vs. Mondrian) could also have led to the different results.

In summary, the results do not support the hypothesis that inter-ocular latency differences in some individuals explain the relatively weak suppression observed in these individuals under typical conditions, compared to others who are stronger suppressors. Such differences in thresholds measured under CFS must indicate intrinsic differences in the strength of competitive inter-ocular interactions that cause suppression, and the reason for this remains to be discovered.

Chapter 5

Experiment 5: Effect of short-term monocular deprivation on inter-ocular suppression[1]

5.1 Introduction

In contrast to the shift in ocular dominance in favour of the non-deprived eye in young animals following prolonged disruption of monocular visual input (e.g. Hubel et al., 1977), very brief periods of monocular deprivation in adults can modify visual processing by improving the relative contribution from the previously deprived eye (e.g. Lunghi et al., 2011; Lunghi et al., 2013). For a review of the relevant literature, please refer to Chapter 1, Section 1.11.

[1]The experiment described in this chapter has previously been published as a paper [Wang, McGraw and Ledgeway, 2020a] and in abstract form [Wang, Ledgeway and McGraw, 2019] and presented at the AVA Christmas Meeting, Birkbeck, University of London, December 10, 2018.

The aims of this study were threefold. The first was to replicate previous findings that brief periods of monocular deprivation alter the relative contribution of the two eyes to perception during binocular rivalry, in favour of the eye that has been patched (Lunghi et al., 2011; Lunghi et al., 2013). The difference is that a light-tight opaque patch was used here—all visual input is eliminated using this type of patch, in contrast to the previously used translucent lens whereby luminance is preserved[2]. Second, the effect of short-term monocular deprivation on eye dominance was also measured using an objective, forced-choice task in a CFS paradigm. An advantage of the CFS paradigm is that, unlike rivalry, the contribution from each eye can be measured independently. Moreover, the results of Experiment 1 suggested that although there was a positive association between the depth of suppression produced by CFS and that under BR, the sign or magnitude of eye dominance measured with the two paradigms was not necessarily consistent for an individual. Whether short-term monocular deprivation affects eye dominance estimated through BR and CFS in the same manner remains unknown. Finally, we asked whether the binocular changes in eye dominance originate from changes in monocular contrast gain of one or both eyes prior to any inter-ocular interactions. Therefore, whether the monocular contrast increment threshold of each eye is altered was also examined in this study.

[2]Although some studies also used an opaque patch, they have not investigated its effect on sensory eye dominance measured with BR (Chadnova et al., 2017b; Zhou, Clavagnier, & Hess, 2013).

5.2 Methods

Six observers participated in this experiment (age range: 22–49 years, one female). Several measures of sensory eye dominance were obtained. Interocular suppression under CFS and the monocular contrast sensitivity of each eye were measured using the probe detection task (see Figure 2.4), as the contrast increment thresholds to detect the location of the test probe. In addition, the temporal dynamics during sustained BR were recorded using the percept tracking task. The stimuli used in both tasks consisted of a noise pattern in one eye and a grating stimulus in the other eye. For a detailed description of apparatus, stimuli and tasks used in this experiment, see Chapter 2, Sections 2.2, 2.3.1 and 2.3.3.

All measurements were made both before patching and immediately after a 150-minute period of occluding one eye with an opaque eye patch that deprived the eye of all visual information. For both pre- and post-deprivation testing, all the conditions (including the BR and CFS measurements, monocular increment thresholds and both configurations of eye of presentation) were completed in a pseudorandom order, to counterbalance any effect of testing order. As the effect produced by monocular patching wanes over time (see Lunghi et al., 2013), the post-patching measurements were taken within a window of 35 minutes after the patch was removed, completed over three sessions separated by at least 24 hours. During monocular deprivation, the participant's non-dominant eye was patched (normal activities allowed), which was the eye more susceptible to CFS (i.e. higher threshold) indicated by the results from the pre-patching measurement.

Although a response for a mixed percept was recorded in this study, the dynamics associated with it were not analysed. However, it was taken into

account when calculating the metrics for the other two percepts because it typically occupies some proportion of time in a particular trial (i.e. the sum of proportions for the exclusive noise and exclusive grating percepts never reached one).

5.2.1 Mixed-effects model analysis

The effects at the group level were statistically evaluated using a mixed-effects model analysis. Linear models were fitted to the data using the function *fitlme* in MATLAB (MathWorks, version R2017a). These models consisted of both fixed effects and subject-dependent random effects, where all random effects were assumed to be uncorrelated with one another.

For the mean phase duration, or the predominance measured with the BR task, the model comprised fixed effects of $Percept$ (noise vs. grating), Eye (patched vs. non-patched), $Time$ (pre- vs. post-patching) and the interaction of all combinations. Intercepts and slopes for all these predictors were included for the random effects. In addition, separate models were then constructed with the data for each eye, including a fixed effect of $Time$ and random effects of the intercept and the slope for $Time$.

For the thresholds measured with the probe detection task, the model incorporated fixed effects of Eye (patched vs. non-patched), $Time$ (pre- vs. post-patching), and their interaction, and random effects of these factors plus the intercept. This analysis was performed for both the monocular contrast increment thresholds, and the depth of inter-ocular suppression evoked by CFS (after discounting the monocular threshold of the corresponding eye), using the following equation:

$$Suppression = 20 \times log_{10}(\frac{Threshold_{CFS}}{Threshold_{Monocular}}). \tag{5.1}$$

In an analogous manner to the BR data, separate mixed-effects models were subsequently constructed for the patched eye and the non-patched eye, to evaluate the effects of monocular patching on each eye. The models included a fixed effect of $Time$ and random effects of the intercept and the slope for $Time$.

Furthermore, an informal analysis with mixed-effects models was conducted to investigate if the data replicate the decay of the patching effect over time observed by Lunghi et al. (2013) (see Figure 1.25). This analysis was performed for the post-patching measurements, including the BR phase duration and predominance for each type of exclusive percept (i.e. noise and grating), and the monocular and CFS thresholds. The time since the removal of the eye patch (within each of the 3 testing sessions) was coded according to the time stamp of the raw data files (one file corresponds to a one-minute trial of the BR percept tracking task or a run of the CFS task containing one staircase). Each mixed-effects model comprised fixed effects of $Time\ course$ and Eye, and their interaction, and a random intercept and random slopes for all predictors.

5.3 Results

Distributions of phase durations (i.e. probability density functions, PDF; bin size: 0.2) are shown in Figure 5.1 and Figure 5.2, for every participant. Each has been normalised to the individual's mean duration measured before patching, for exclusive noise and grating percepts, respectively. The corresponding cumulative density functions (CDF) were then fitted with a gamma distribution defined by Equation 2.5[3]. Although the CDF of the

[3]For the details of the fitting procedures, see Chapter 2, Section 2.4.

distributions was fitted, the fitted curves are plotted as PDF in Figure 5.1 and Figure 5.2, using the estimated parameters based on the CDF fits, to allow direct comparison to the results presented in previous work by Lunghi et al. (2013). On the whole, there is a rightward shift in the distribution for the stimulus shown to the deprived eye and a leftward shift in the other eye, consistent with the findings of Lunghi et al. (2013). These changes also apply to the normalised phase durations pooled across the participant group (Figure 5.3).

Lunghi et al. (2013) found that the ratio of the shape parameter (ρ) to the scale parameter (λ), which describes the mean of the gamma distribution, was approximately unity in the absence of prior deprivation (Figure 5.4). However, it was increased for the deprived eye and decreased for the non-deprived eye after monocular deprivation. The time course of this effect resembles that for the changes in the mean phase duration for each eye (compare Figure 5.4 and Figure 1.25; Lunghi et al., 2013). In the present study a similar effect on the ratio of ρ to λ was observed, as depicted in Figure 5.5. For both exclusive noise and exclusive grating percepts, the ratio for each eye was close to unity before patching, with little inter-ocular or inter-individual variation (mean data across all the subjects shown by the big crosses). The ratio was altered after monocular patching, in opposite directions for the two eyes—it was increased for the patched eye (i.e. an upward shift) and decreased for the non-patched eye (i.e. a leftward shift). Based on the meaning of ρ/λ, these results imply an increased mean exclusive phase duration for the patched eye and a decreased mean duration for the non-patched eye. Nevertheless, not all observers showed a pronounced effect, and there were larger inter-individual variations compared to the pre-patching level (see S7, noise percept, and S4, grating percept).

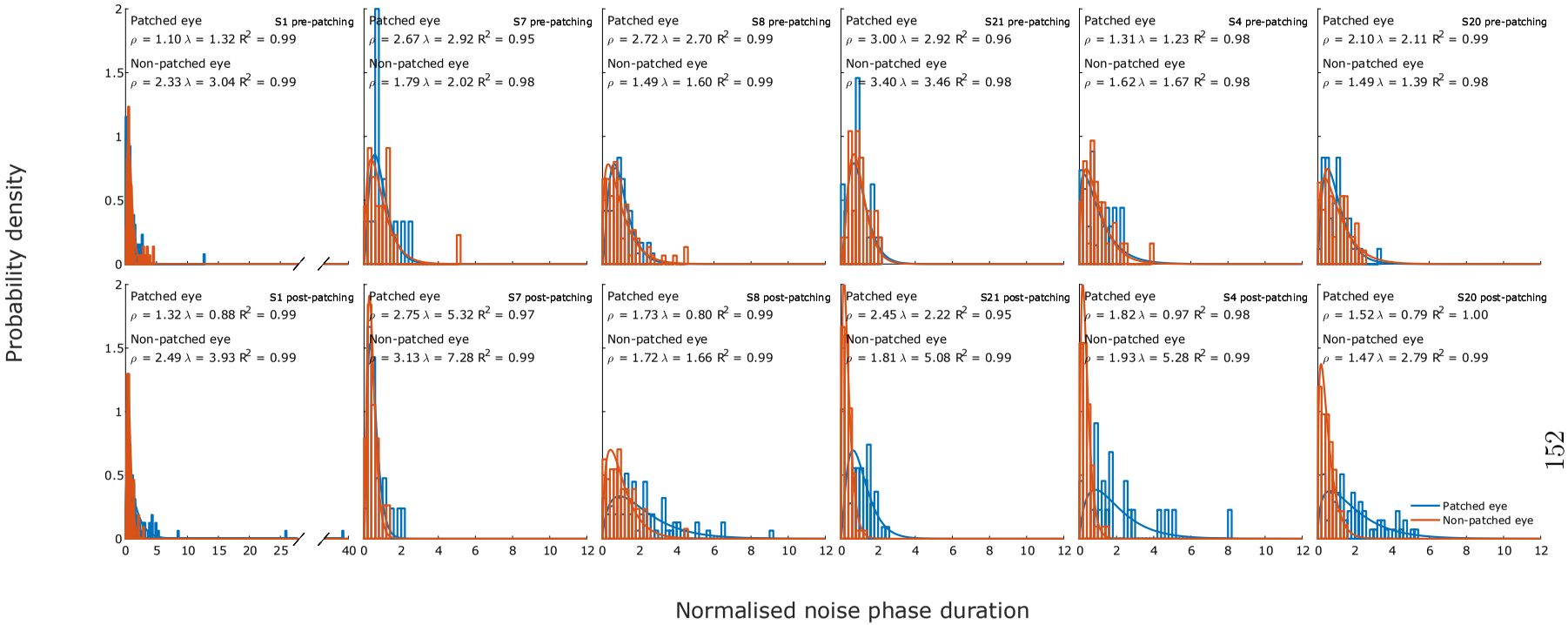


Figure 5.1: Phase duration distributions for exclusive noise percepts experienced by the patched eye (blue) and non-patched eye (orange), plotted as probability density functions, separately for pre- (upper panel) and post-patching measurements (lower panel), and for each individual in Experiment 5. The phase durations were normalised to each observer's mean noise percept duration prior to monocular patching. Note that the scale of abscissae was made consistent across individuals except for S1 due to remarkable differences from other observers. The curves are plotted as the gamma PDF, using the parameters estimated from fitting with gamma CDF. The fit results, including the estimated parameters, ρ and λ, and the goodness of fit indicated by R^2 are shown.

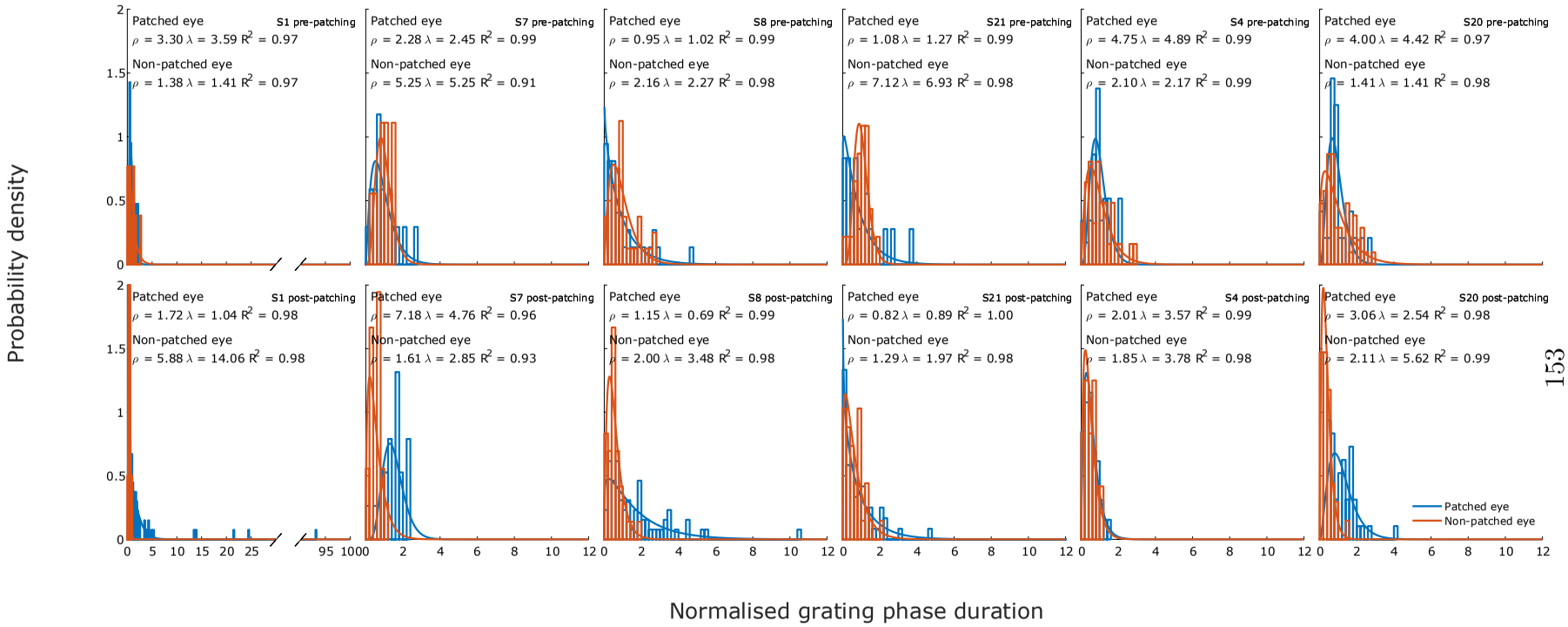


Figure 5.2: Individual normalised phase duration distributions for exclusive grating percepts in Experiment 5. Conventions are the same as in Figure 5.1.

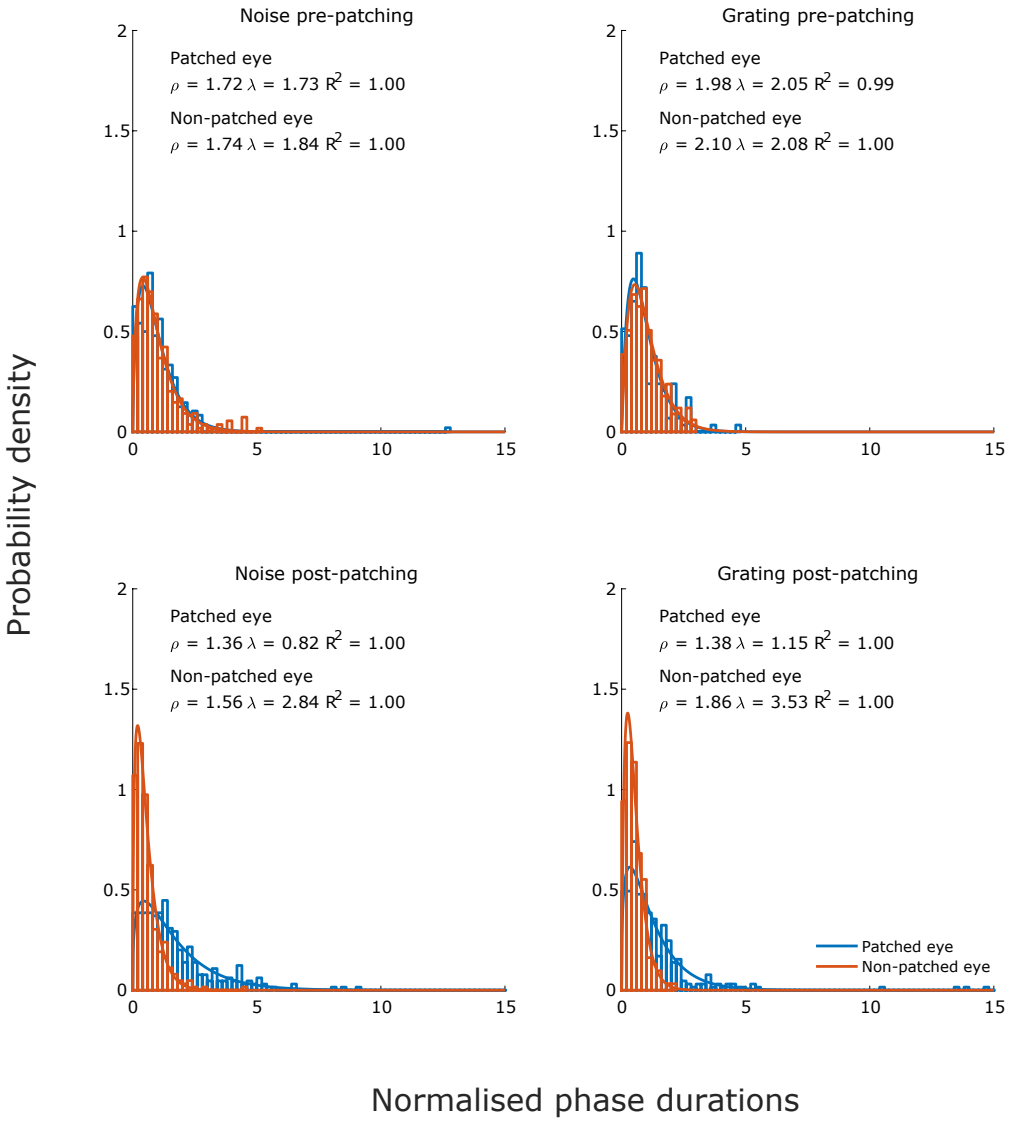


Figure 5.3: Normalised phase duration distributions for exclusive noise or grating percepts pooled across all the six subjects in Experiment 5. Conventions are the same as in Figures 5.1 and 5.2.

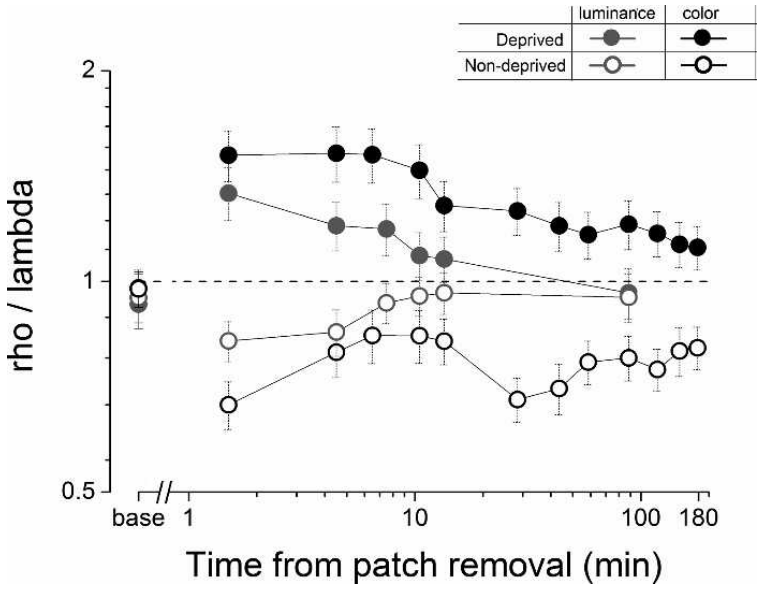


Figure 5.4: The ratio of rho to lambda (estimated parameters of the gamma distributions of normalised BR exclusive phase durations) following 150-minute monocular deprivation as a function of the time since patch removal, for the deprived eye and the non-deprived eye, when either achromatic or chromatic stimuli were tested (see Figure 1.24 for the distributions and parameters for the achromatic condition). The ratios measured prior to monocular deprivation were also shown (base). The dashed line marks the unity. Adapted from Lunghi et al. (2013).

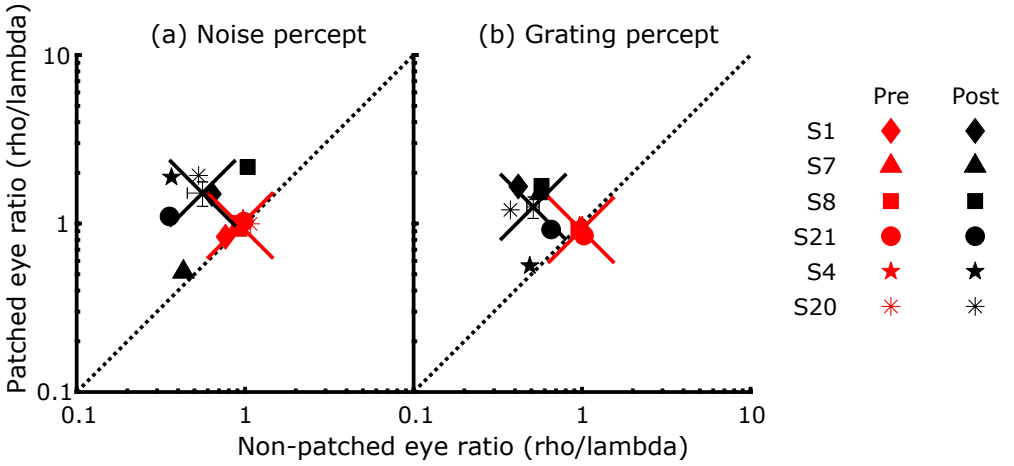


Figure 5.5: Ratios of the shape parameter (ρ) to scale parameter (λ) for the fitted phase duration distributions of (a) exclusive noise and (b) exclusive grating percepts, for pre- (red) and post-patching measurements (black). The ordinates indicate the ratios for the patched eye and the abscissae show those for the non-patched eye. The dotted lines indicate equal ratios for the two eyes. Small symbols represent data for different individuals. The grand means calculated across all participants are marked by the big crosses (error bars: ± 1 SEM).

The mean phase durations and proportion of time that each percept was perceived (i.e. predominance), before (red) and after patching (black), are plotted in Figure 5.6a–d for the patched eye (ordinate) and non-patched eye (abscissa). A diagonal line with unity slope marks the balance of the two eyes, and data points deviating from this line indicate dominance of one eye (see figure legend). As can be seen, the mean phase duration (Figure 5.6a, b) and predominance of each exclusive percept (Figure 5.6c, d), were increased when the corresponding stimulus was presented to the patched eye (i.e. an upward shift), or decreased when presented to the non-patched eye (i.e. a leftward shift). The absolute changes in each eye's measures appear variable across individuals. These results were evaluated by permutation tests, comparing the pre- and post-patching exclusive phase durations (mean or median), for the patched and non-patched eyes separately[4]. The p values

[4]For each individual, the raw durations were permuted between the pre- and post-

are shown in Appendix A, which also indicated that the changes were not uniform in terms of which eye was affected—originating in the patched eye, in the non-patched eye, or both for the subjects tested. Therefore, to extract a more suitable metric capturing the universal pattern of effects across subjects, the ratio of the eye dominance after patching over that prior to patching was calculated using the following equation (a similar deprivation effect index has been previously used by Lunghi, Emir, Morrone, and Bridge (2015)):

$$Patching\ effect = 20 \times log_{10}(\frac{Patched\ eye_{post}/Nonpatched\ eye_{post}}{Patched\ eye_{pre}/Nonpatched\ eye_{pre}}), \quad (5.2)$$

where a $Patching\ effect$ index of zero denotes no difference between the pre- and post-patching measures and non-zero values indicate a change in the degree of eye dominance as a consequence of patching. Note that for BR dynamics a positive index signifies enhanced dominance of the eye that was previously patched, whereas for threshold measures the converse is true.

patching measurements. The difference in mean/median duration between these two conditions was then calculated for the permuted data. This permutation procedure was repeated 10000 times. Consequently, a p value assessing whether the measures in the two conditions were significantly different was computed as the proportion of the total permutations when the mean/median difference (absolute value) calculated from the permuted data was greater than that using the original data.

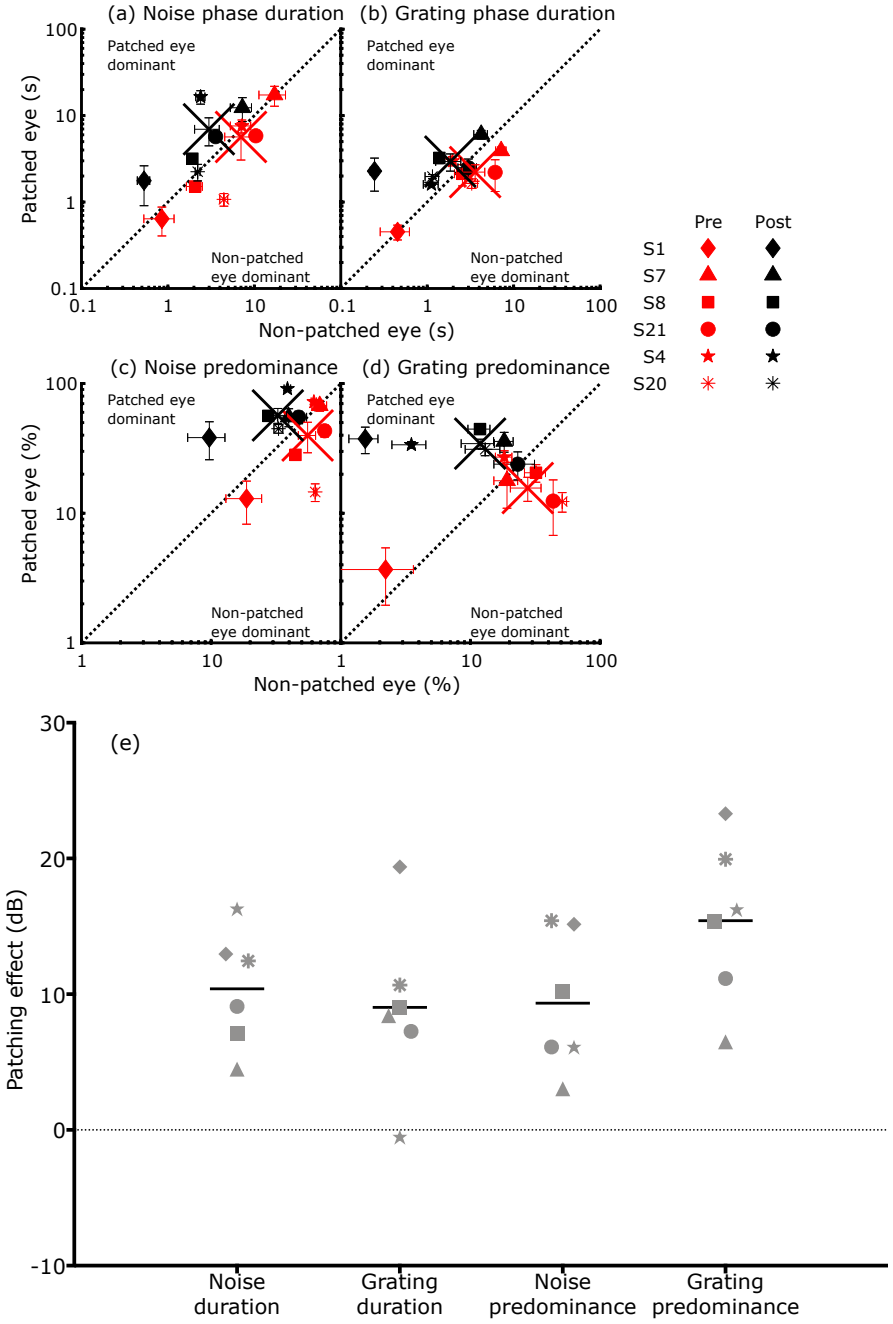

(a) Noise phase duration
(b) Grating phase duration
(c) Noise predominance
(d) Grating predominance
Patched eye dominant
Non-patched eye dominant
Patched eye (s)
Non-patched eye (s)
Patched eye (%)
Non-patched eye (%)
100
10
1
0.1
Pre
Post
S1
S7
S8
S21
S4
S20
(e)
Patching effect (dB)
30
20
10
0
-10
Noise duration
Grating duration
Noise predominance
Grating predominance

Figure 5.6 *(previous page)*: The changes of BR dynamics produced by monocular patching in Experiment 5. The pre- (red) and post-patching measurements (black) for the patched eye versus non-patched eye are shown in (a)–(d). Small symbols represent data for individuals. The mean data across all participants are marked by the big crosses. (a) Mean phase duration for exclusive noise percepts. (b) Mean phase duration for exclusive grating percepts. (c) Proportion of time (i.e. predominance) that the noise was being perceived. (d) Grating predominance. The dotted line depicts where the patched eye exhibited equal strength to the non-patched eye. Patched eye dominance is indicated by data points that fall above the diagonal dotted line, while data points below the line show non-patched eye dominance. Horizontal and vertical bars represent the ± 1 SEM. The $Patching\ effect$ index (Equation 5.2) quantifying the degree of eye dominance for the post-patching measurement relative to that for the pre-patching measurement is shown in (e), in terms of BR mean phase duration and predominance for each exclusive percept. Individual data are shown as grey symbols. The horizontal solid lines show the grand means calculated across all six participants for the corresponding condition. The horizontal dotted line represents no difference between measures obtained before and after monocular patching. See text for more details.

The resultant index for all BR measures is plotted in Figure 5.6e. The plot essentially reflects the results shown in Figure 5.6a–d, but it extracts a common component that captures the patching effect across individuals and conditions (i.e. changes in relative eye dominance). The computed indices for these BR measures illustrate an obvious shift in the relative sensory eye dominance towards the previously patched eye with monocular deprivation in this group of participants. In addition, permutation tests were conducted to statistically evaluate the difference, for each observer, between the eye dominance for pre-patching measurement and that for post-patching measurement (for each type of exclusive percept separately). The eye dominance here was computed as the ratio of mean patched eye duration to that of the non-patched eye[5]. As shown in Table 5.1, the ratio was

[5]The raw durations were first permuted between the pre- and post-patching measurements for each eye. The eye dominance ratio for each condition was then obtained

significantly different for at least one type of exclusive percept for every subject.

Table 5.1: The results of permutation tests (number of permutations: 10000) comparing eye dominance prior to and following monocular patching, indexed by the ratio of mean patched eye duration to mean non-patched eye duration, for exclusive noise and exclusive grating percepts. The p values are shown for each individual.

Observer	Noise	Grating
S1	.001	.079
S7	.433	.007
S8	.001	$< .001$
S21	.001	.256
S4	$< .001$	.672
S20	$< .001$	$< .001$

The results of mixed-effects model analysis for the BR mean phase duration showed significant main effects of *Percept* ($t_{(40)} = 3.84, p < .001$) and *Time* ($t_{(40)} = -2.07, p = .045$), and an interaction effect between *Eye* and *Time* ($t_{(40)} = 7.71, p < .001$). Overall, the exclusive percept phase duration was longer for the noise than that for the grating stimulus and was slightly shortened after patching. Moreover, the analyses of the models including only the effects of *Time* for the two eyes separately suggested that the decrease in mean phase duration for the non-patched eye ($t_{(22)} = -2.41, p = .025$) was more consistent across individuals than the changes for the patched eye ($t_{(22)} = .647, p = .524$).

The results for the model constructed for predominance revealed a sig-

using the mean permuted durations, and the difference in that ratio between conditions was calculated. This permutation procedure was repeated 10000 times, and a p value evaluating whether the ratios obtained in the two conditions were significantly different was subsequently computed as the proportion of times when the ratio difference (absolute value) calculated from the permuted data was greater than that calculated using the original data. This analysis was only performed in terms of BR phase duration but not predominance or the threshold data as the number of observations for the latter two cases was not sufficient to conduct permutations.

nificant main effect of $Percept$ ($t_{(40)} = 6.52, p < .001$), and $Eye \times Time$ ($t_{(40)} = 9.39, p < .001$) and $Percept \times Eye \times Time$ ($t_{(40)} = 2.05, p = .047$) interactions. Like phase duration, the noise stimulus was also perceived for more time in total than the grating. When looking at the effect of $Time$ on each eye, the results showed an increased predominance for the patched eye after monocular deprivation ($t_{(22)} = 2.42, p = .024$), and decreased predominance for the non-patched eye ($t_{(22)} = -2.77, p = .011$). The three-way interaction associated with predominance is more complicated to interpret, and further breakdown of the term suggested that it may result from the larger difference between the noise and grating predominance viewed by the non-patched eye relative to that presented to the patched eye; this was only true for the pre-patching measurements, and was absent when tested after patching.

In a similar vein, the individual's mean increment threshold measured before and after patching, in the monocular condition and under CFS, is shown in Figure 5.7a and b, for the patched and non-patched eye. The results in Figure 5.7a suggest that monocular increment thresholds, measured in each eye in the absence of the suppressing noise pattern in the other eye, were minimally affected, and that there was no consistent change across individuals. The data points for all observers are close to the unity line. In contrast, the effect of patching was revealed when measured under CFS (Figure 5.7b). The threshold for the previously patched eye decreased after patching, for all participants except S1, who exhibited very little suppression for either pre- or post-patching measurements. On the other hand, the suppression measured with the non-patched eye was not consistently influenced across observers. An index of $Patching\ effect$ was also computed for these thresholds (Figure 5.7c). The sensory eye dominance associated

with the inter-ocular suppression evoked by CFS, on average, was moved towards the patched eye following monocular deprivation, but this effect was absent when the threshold was measured monocularly. Unlike the mixed effects found with BR dynamics—an enhancement of the patched eye, a diminution of the non-patched eye, or a combination of both—the patching effect revealed with the CFS task was largely driven by the reduction in susceptibility of the patched eye to inter-ocular suppression (see Figure 5.7b).

Whilst the $Patching\ effect$ for the monocular increment threshold was very similar for all observers, there were some differences between individuals for conditions involving inter-ocular suppression. Notably, individuals exhibiting larger patching effects in the CFS condition also tended, in general, to be more susceptible to CFS (see Figure 5.7). This is probably because the patching effect measured with CFS manifested in reduced inter-ocular suppression of the patched eye and those observers who were already very resistant to suppression before patching were therefore less able to exhibit a reduction in this effect (cf. S1).

For the mixed-effects model analyses of the contrast increment thresholds measured with the probe detection task, the results showed that none of the factors included in the linear model significantly predicted monocular thresholds ($Time$: $t_{(20)} = -0.11, p = .913$; Eye: $t_{(20)} = -0.20, p = .840$; $Eye \times Time$ interaction: $t_{(20)} = -0.46, p = .651$). For the $Suppression$ index calculated using Equation 5.1, in contrast, there was a significant main effect of $Time$ ($t_{(20)} = -2.36, p = .029$) and its interaction with Eye ($t_{(20)} = -2.77, p = .012$). When averaged across eyes, a decrease in inter-ocular suppression was revealed after monocular patching. The interaction term is of more interest, suggesting a distinct influence of monocular patch-

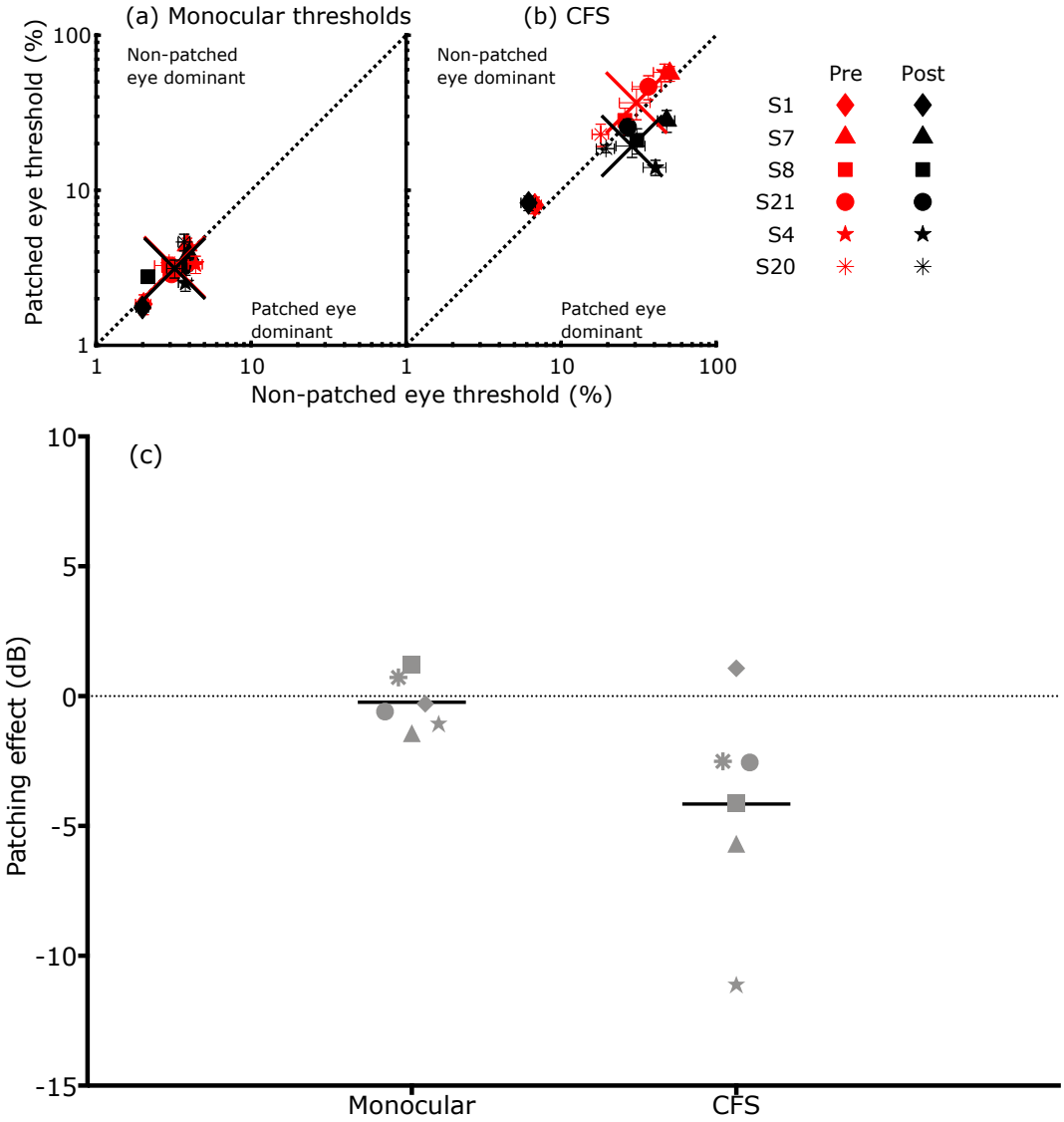


Figure 5.7: The effects of monocular patching on contrast increment thresholds measured with the probe detection task in Experiment 5. The pre- and post-patching measurements of (a) monocular increment thresholds for the patched eye versus non-patched eye and (b) those for the thresholds measured under CFS. (c) *Patching effect* index (Equation 5.2) computed from thresholds measured in the monocular condition and under CFS. Conventions are the same as in Figure 5.6 with the following exception. In (a) and (b) data points falling below the diagonal dotted line indicate patched eye dominance. Note that in (c) the different direction of change in *Patching effect* values calculated with probe thresholds from that for BR temporal dynamics (Figure 5.6e) indicates the same shift in sensory eye dominance (see text for further details).

ing on the two eyes. Furthermore, as expected from Figure 5.7b, the results of separate models for the two eyes showed a decline in suppression after patching only for the patched eye ($t_{(10)} = -3.08, p = .012$), whereas there was no change for the non-patched eye ($t_{(10)} = -.40, p = .70$). This result reinforces the differential effect patching has on the two eyes.

Interestingly, the analysis of the time course of the patching effects suggested that the difference between eyes decayed over the period of testing but only for the contrast increment thresholds measured with CFS. This was indicated by a significant $Time\ course \times Eye$ interaction ($t_{(68)} = 2.81, p = .006$), while no such effect was found for monocular increment thresholds, BR phase duration, or BR predominance for either noise or grating. Specifically, the CFS threshold for the patched eye increased as time passed, meaning a return to the level before patching. There was no systematic time effect for the increment threshold measured for the non-patched eye.

5.4 Discussion

In the current study, monocular deprivation for 2.5 hours altered the relative balance between the two eyes, measured with BR and CFS. Previous research has shown that varying the severity of deprivation (e.g. form vs. light exclusion) results in similar effects on the subsequent contribution of each eye to binocular combination (Zhou, Clavagnier, & Hess, 2013). The current study extends this work to show that opaque patching (cf. translucent patching used by Lunghi et al., 2011; Lunghi et al., 2013) can also bias sensory eye dominance measured using tasks involving inter-ocular suppression where the two eyes' images are not fusible. The results highlight the robustness of this plasticity and suggest that the mode of sensory depriva-

tion does not matter for its effect on BR dynamics.

More importantly, by using a CFS task, this study was able to show that short-term monocular deprivation changed inhibitory interactions between the two eyes, leaving the monocular contrast increment thresholds unaffected. Specifically, the deprived eye became less susceptible to suppression, whereas complementary changes were not found in the other eye. It is worth noting that Sheynin, Proulx, and Hess (2019) reported decreased exclusive dominance for the non-deprived eye's percept during BR with no change in that for the previously deprived eye. This finding may be interpreted in the context of the present result of reduced suppression of the deprived eye as explained as follows. A prominent model of binocular rivalry proposes a mechanism involving mutual inhibition and self-adaptation (see Chapter 1, Section 1.7; H. R. Wilson, 2007). An implication of this idea is that exclusive dominance of one eye's percept is determined by the strength of inter-ocular inhibition of the mechanism encoding the contralateral eye's stimulus. That is to say, Sheynin et al.'s (2019) observation of decreased exclusive dominance for the non-deprived eye's percept was a sign of reduced inhibition of the deprived eye. Indeed, their findings of increased probability of binocular combination and superimposed mixed percepts also point to a reduced level of inter-ocular suppression following short-term monocular deprivation. Furthermore, the attenuated inter-ocular suppression is consistent with the observation of a reduction in resting concentration of an inhibitory neurotransmitter, gamma-Aminobutyric acid (GABA), in primary visual cortex (V1) following monocular deprivation (Lunghi, Emir, et al., 2015). The present results on the time course of post-deprivation measures, indicated that the suppression of the deprived eye recovered over time, whereas the suppression of the non-deprived eye showed no systematic

variations with time once the patch was removed. Thus short-term monocular deprivation leads to a unilateral, non-reciprocal change of inter-ocular suppression.

An explanation of the consequences of short-term monocular deprivation favoured by many researchers is that the modulation of sensory eye dominance arises from reciprocal changes in each eye's contrast gain (Chadnova et al., 2017b; Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). Whilst the current results did show reduced susceptibility of the previously deprived eye to inter-ocular suppression, which is consistent with that idea, the fact that the non-deprived eye is largely unaffected argues against it. This is because inter-ocular suppression, in either direction, is expected to be influenced when the balance in contrast gain between the two eyes changes. The present results indicate that the suppression of each eye is modulated independently by monocular deprivation.

Crucially, the current findings have demonstrated that altered ocular balance cannot be accounted for by changes in monocular contrast increment threshold. The validity of this observation is strengthened by the results that the monocular increment thresholds measured after patching did not vary with time during a testing session. Therefore, it can be concluded that monocular deprivation elicits direct effects on binocular interactions, rather than acting on the monocular contrast gain of each eye which later interactions may be dependent on. Indeed, results from Chadnova et al. (2017b) also revealed that changes in eye dominance could only be seen when stimulated dichoptically, whereas monocular stimulation was not able to reveal the bias. Although some other studies have reported modified monocular thresholds following deprivation (Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013), that the changes in

suppression measured under CFS were the consequences of altered monocular contrast increment thresholds is not a favoured account here for the following reasons. Thresholds were obtained for both monocular and CFS conditions, and the very modest changes in monocular thresholds did not predict the pattern of changes in CFS thresholds (see Figure 5.7a and b). Furthermore, we still found changes in the depth of suppression even after accounting for any variations in monocular thresholds.

It is possible that the inconsistencies in the findings relating to monocular thresholds may have arisen from methodological differences. For example, Zhou, Clavagnier, and Hess (2013), Zhou et al. (2017), Zhou, Thompson, and Hess (2013) used an orientation-identification task to measure monocular contrast thresholds, whereas here contrast increment thresholds were measured using a location judgement task. In Zhou, Clavagnier, and Hess's (2013) and Zhou, Thompson, and Hess's (2013) studies, only 2 or 3 subjects were tested and the observed changes in monocular thresholds were relatively small[6]. Zhou et al. (2017) tested the same number of subjects (i.e. 6) as the current study, but their analyses only examined differences between the two eyes after the patch was removed (i.e. a main effect of eye). Whether or not monocular thresholds for each eye were altered by patching was not statistically evaluated.

One point to note is that contrast increment thresholds were measured to assess monocular gain. It may be argued, however, that the unaltered monocular thresholds might have been due to an unchanged signal-to-noise ratio, and changes in monocular contrast gain remained possible. Whilst a suprathreshold binocular contrast matching task, like the one used by Zhou,

[6]Zhou, Thompson, and Hess (2013) examined the effect of monocular deprivation on monocular thresholds in three amblyopic subjects. Two of the subjects showed significant changes, whereas reciprocal changes in the two eyes were not always present. The third subject did not show any significant changes in monocular thresholds.

Clavagnier, and Hess (2013), can quantify the perceived contrast of each eye following deprivation, this approach cannot determine whether the locus of this effect is binocular or monocular. Nevertheless, as discussed earlier, a change in the monocular contrast gain of either eye would predict altered depth of suppression measured in both eyes, a phenomenon not supported by our results.

The findings in the context of binocular rivalry appear to be consistent with models where inter-ocular suppression is driven by opponency units detecting conflict between the two eyes' inputs (see Figure 1.8; Katyal et al., 2016; Katyal et al., 2018; Said & Heeger, 2013). The neurophysiological basis is thought to be neurons that can compute either the sum or difference in luminance input between the eyes (Smith III, Chino, Ni, Ridder, & Crawford, 1997). Psychophysical evidence suggests that these summation and differencing mechanisms are independently adaptable (May & Zhaoping, 2016; May, Zhaoping, & Hibbard, 2012). This form of opponency provides a plausible account for the present results in that the strength of inter-ocular inhibition may be changed by directly modifying the activity of opponency channels without affecting monocular processing. A signature of this class of model is the prediction of weaker inter-ocular inhibition after selective adaptation of the opponency channel. In binocular rivalry studies, this notion receives empirical support from the observation of increased probability of mixed perception over prolonged exposure to non-fusible dichoptic stimulation (Klink et al., 2010; Said & Heeger, 2013). Here, the dampened activity in the opponency channel from adaptation produces lower inter-ocular inhibition and over time becomes less able to sustain exclusive dominance of one eye's percept over the other. One way of evaluating whether opponency channels are modified by short-term monocular deprivation would be

to look at changes in rivalry perception (dominance versus mixed percepts) before and after patching. However, the current experimental design, where the order of measurements was randomised and intermingled between conditions is not well suited to examine this. Further investigations are needed to address this issue more directly. At present an opponency-based scheme cannot not be ruled out, but it is not the only possible explanation.

Alternatively, the findings of these experiments can be interpreted within the framework offered by gain control models of binocular vision (Ding et al., 2013a, 2013b; Ding & Sperling, 2006; Meese et al., 2006). These models are based on the idea that the visual system relies on contrast gain control to optimise sensitivity (Gardner et al., 2005; Ohzawa, Sclar, & Freeman, 1985). Specifically, the input from each eye (C_L and C_R for the left and right eye, respectively) undergoes divisive inhibition before the monocular outputs from the two eyes' channels are summed for binocular perception. Figure 5.8 illustrates the components of such types of model in which the current results may be explained. If deprivation only acts on the inter-ocular suppression of the patched eye (say the left eye) by the non-patched eye (S_{RL}), as indicated by the present results, the monocular gain of the patched eye (ϵ_L) will not be altered. Note that the models suggest a dependence of the inter-ocular suppression of one eye (S_{RL} or S_{LR}) on the other eye's gain (ϵ_R or ϵ_L), known as inter-ocular gain control. This predicts that the reduced suppression of the patched eye may result from a decreased gain of the non-patched eye (possibly due to a lowered gain efficiency, μ_R), which is, however, not the pattern seen in the present results. These results, therefore, indicate an extra parameter of the intrinsic susceptibility of the eye to inter-ocular inhibition (I_{RL} and I_{LR}), that weights the gain-dependent inter-ocular suppression component (S_{RL} and S_{LR}), and which

can be adjusted by short-term monocular deprivation. This notion can be incorporated into the first stage before binocular summation of Meese et al.'s (2006) two-stage model, by including independent weights to monocular and inter-ocular gain control such that the latter is subject to the influence of monocular deprivation (see also Spiegel, Baldwin, and Hess, 2017).

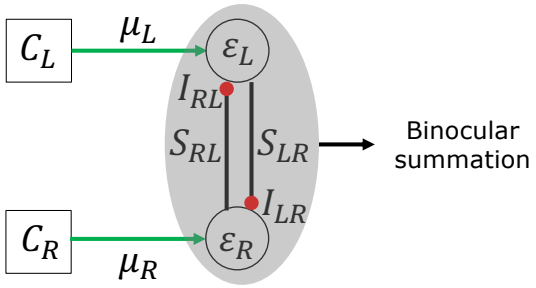


Figure 5.8: A schematic model within which the current findings may be interpreted. The subscripts L and R indicate the parameters for the left and right eyes, respectively. C_L and C_R (boxes) represent the input strength of the two eyes (i.e. contrast). μ_L and μ_R (green arrowed paths) are the gain efficiency of the two monocular channels. ϵ_L and ϵ_R (circles) are the monocular contrast gain for the two eyes. The gain of an eye is determined by both the input strength in this eye and the gain efficiency of the corresponding monocular channel. I_{RL} and I_{LR} (red dots) are the intrinsic susceptibility of each eye to inter-ocular inhibition and are independent of the monocular gain. S_{RL} is the output suppression of the left eye by the right eye and S_{LR} is the inter-ocular suppression in the converse direction (black lines ending in a dot). This output suppression of an eye depends on both the intrinsic susceptibility to inter-ocular inhibition of this eye and the monocular contrast gain of both eyes. It is assumed that the output following such inhibitory inter-ocular interactions (shaded area) will subsequently undergo binocular summation.

The present study extends the finding of short-term (opaque) patching on binocular contrast combination between fusible stimuli to binocular rivalry between non-fusible stimuli. As discussed in Chapter 1, Section 1.11.3, Baldwin and Hess (2018) have demonstrated a reduction in dichoptic masking of the previously deprived eye following short-term monocular deprivation, when the two eyes' stimuli had either identical or orthogonal

orientations. However, the deprivation effects measured in these two conditions did not significantly correlate across the group of participants tested, implying separate processes underpinning the changes found in fusible and non-fusible conditions (see Figure 1.28). It is therefore reasonable to place a caveat on the conclusion—although similar consequences on binocular rivalry and binocular contrast combination were obtained following monocular deprivation, these do not necessarily posit a common mechanism of plasticity.

Binocular phase combination has been frequently used to assess the effect of deprivation on sensory eye dominance (Bai et al., 2017; Y. Wang et al., 2017; Yao et al., 2017; Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2014; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013). However, there may be multiple binocular processes involved in this task, making it hard to disentangle the underlying mechanisms. Evidence suggests that binocular fusion and inter-ocular suppression are both likely to occur for a blurred, horizontally-oriented edge that has a small vertical disparity between the two eyes, but these two consequences are mutually exclusive (Georgeson & Wallis, 2014). When it comes to using phase combination as a measure of binocular perception, we cannot tell whether a biased perception occurs because the two vertically offset monocular images are fused to form an imbalanced binocular percept, or because of suppression of one of the images. The probability of suppression is even higher when there is an imbalance in contrast between the two eyes' inputs (Georgeson & Wallis, 2014). Although fusion and suppression both reflect aspects of each eye's contribution to perception after binocular interactions, they may be differentially affected by deprivation.

The use of opaque patching suggests that the plastic changes observed

are mostly input driven. There may be other circumstances, where other forms of inter-ocular imbalance are involved. For example, Kim et al. (2017) have illustrated that both a lack of conscious awareness in one eye, rendered by CFS, and a reduction in contrast energy relative to the other eye, are able to induce a subsequent bias favouring the affected eye. In addition, the shift in eye dominance can be demonstrated when the inputs to the two eyes have matched Fourier amplitude spectra but scrambled spatial phases (Bai et al., 2017). One possibility is that the scrambled image is less useful than the normal image viewed by the other eye, and the participant selectively attends to the untreated eye's input. In this view it is the imbalanced allocation of attention that drives the subsequent, compensatory, enhancement of the treated eye. It is reasonable to assume that the consequences of an imbalance in attention between eyes may only be revealed with dichoptic stimuli that are not fusible. This is because there is no competition between eyes in terms of attention when tested with fusible stimuli, and compensatory processes may not be triggered. Nonetheless, the hypothesis that higher-level factors may also play a role in sensory eye dominance plasticity is still preliminary and systematic examinations are needed, which will be explored in chapters that follow.

On the basis of the current sample, we were able to compare the patching effects assessed with BR and CFS, two processes that are strongly related (see Chapter 3). Yet, the manner in which these two types of inter-ocular suppression are affected by deprivation may not be the same. Unlike the unilateral changes under CFS, for BR mixed effects were found: an enhancement of the deprived eye, a diminution of the non-deprived eye, or a combination of both contributed to the alteration of sensory eye dominance. Similar mixed patterns of changes in phase duration of each eye's

image were also observed in other studies examining the effect of short-term monocular deprivation on BR (e.g. visual inspection of Figure 3a in Binda & Lunghi, 2017). This implies that the relative, but not absolute strength, of each eye's contribution is more important for BR. In support, using principal component analysis (PCA), Sheynin et al. (2019) have demonstrated that a principal component representing relative eye dominance explained the changes in BR dynamics produced by monocular deprivation whilst another principal component representing exclusive dominance independent of eye of origin did not significantly predict the results. This conclusion links to the finding of a discrepancy between eye dominance manifested in CFS and BR in Experiments 1 and 2 (see Figures 3.6 and 3.7), pointing to potentially different mechanisms.

To summarise, this study has illustrated a boost to one eye that has been deprived of input for a few hours, relative to the other eye, in two tasks involving inhibitory binocular interactions. Importantly, we have shown that this shift in sensory eye dominance is specifically due to reduced inter-ocular suppression (inhibition) of the deprived eye. This is conceivably relevant to the notion that the restricted plasticity of adult brains is associated with an altered excitation/inhibition balance (i.e. increased inhibition) compared to developing brains (Chen et al., 2011; Keck et al., 2011; van Versendaal & Levelt, 2016). Recent studies in amblyopia have shown abnormally reduced inter-ocular suppression of the fellow eye by the amblyopic eye (Ding et al., 2013a; Huang et al., 2012; Shooner et al., 2017; Zhou et al., 2018). The present findings imply that inter-ocular suppression can be modulated for each eye separately, which may be relevant when the level of inter-ocular suppression has to be adjusted in only one eye. One implication is that in adults with amblyopia, an effective method may be to occlude the amblyopic

rather than unaffected eye for short periods of time.

Chapter 6

Is deprivation of low-level input necessary to shift eye dominance?[1]

6.1 Introduction

The importance of investigating the effects of various monocular manipulations on sensory eye dominance has been noted in Chapter 1 (see Section 1.11.5). The present study aimed to compare the consequences of different types of short-term monocular treatment on binocular rivalry. We chose to measure BR rather than CFS because it is a quicker way of quantifying sensory eye dominance.

The results of Experiment 5 demonstrated that opaque patching was able to strengthen the relative contribution of the previously patched eye to BR. The stimuli used in that task were relatively complex, however, consist-

[1]The experiments described in this chapter have previously been published, in part, in abstract form [Wang, McGraw and Ledgeway, 2019c] and presented at the 42nd European Conference on Visual Perception (ECVP, 2019).

ing of spatially two-dimensional visual noise and a sinusoidal grating, which are not conventionally used to quantify sensory eye dominance. The noise stimulus, contained both horizontal and vertical contours, and hence may have potentially engaged both cross- and within-channel inter-ocular suppression, which are proposed to be relatively independent processes (Baldwin & Hess, 2018). In the current study, therefore, a pair of orthogonal gratings were used instead to trigger rivalry experience. Meanwhile, utilising identical stimuli and procedures, changes in eye dominance following monocular patching achieved with a translucent lens (producing a homogeneous field known as Ganzfeld) or a prism that inverted the image, were also assessed in the same group of participants. Whereas opaque patching deprives the eye of all visual input, translucent patching only eliminates contour information but provides matched luminance between the two eyes. Placing an inverting prism over one eye leads to matched luminance and contrast energy in the two eyes, while preventing binocular fusion. Whilst scrambling the phase information in one eye without altering the Fourier amplitude can also realise balanced luminance and contrast between the two eyes (see Bai et al., 2017), the inverting prism has the advantage of maintaining the spatial phase relationships between components (preserving object shape information), despite inversion of the image. This minimises the inter-ocular mismatch in low-level input, revealing any impact of higher-level factors. Investigating these three types of monocular treatment in the same study, therefore, allowed us to directly compare their effects on subsequent eye dominance measures, and hence to decouple the roles of low-level and high-level (cognitive) mechanisms in determining inter-ocular balance. In addition, another objective was to evaluate the time course of the effects produced by all three types of monocular treatment (which was

only preliminarily examined in Experiment 5). The temporal profile of BR responses may serve as a signature for distinct mechanisms.

6.2 Experiment 6: How do different types of monocular treatment affect subsequent sensory eye dominance?

6.2.1 Methods

Seven participants, who had normal or corrected-to-normal vision took part in the study (age range: 23–50 years, one female). S4 and S6 were only available to complete the opaque and Ganzfeld patching conditions, and S21 only participated in the inverting prism condition. The remaining participants completed all three treatment conditions. Sensory eye dominance was assessed by measuring temporal dynamics during sustained BR between orthogonal gratings, using a perceptual tracking task. For the description of apparatus, stimuli and tasks used in this experiment, see Chapter 2, Sections 2.2 and 2.3.3.

The subjective experience during BR was measured continuously for 30 minutes, with a brief break every three minutes. This measurement was completed both in the absence of (i.e. baseline), and immediately following monocular treatment for a duration of 150 minutes. The effects of three types of treatment were examined: First, with a black, opaque eye patch, all visual input to one eye was eliminated. Second, participants wore a pair of standard safety goggles, where one of the lenses was abraded with fine-grain sand paper to create a Ganzfeld impression. That is, all contour information was removed (i.e. no contrast energy) such that subjects could

not, for example, count fingers at a distance of 10 cm, whilst luminance was preserved (but was attenuated by approximately 15% as measured by a spot photometer). In addition, for a third treatment condition, a Porro prism was placed over one eye using a trial frame, to invert the image viewed by that eye. In this way the two eyes' images were matched in luminance and contrast whilst binocular fusion was prevented[2]. Although the field of view through the inverting prism was limited, subtending 33.40° vertically and 28.01° horizontally, it was sufficiently larger than the subtended angle of the visual displays used for presenting the stimuli. The monocular treatment was conducted at least twice for each eye for each treatment condition.

The phase durations were used for analysis. However as was the case in Experiment 5, only the exclusive percept phases were analysed. The raw phase durations, binned every three minutes, were pooled across all testing sessions of the corresponding treatment condition, and grouped based on whether the stimulus was presented to the treated eye or the non-treated eye, discounting any existing biases of eye and/or orientation. As there were marked individual differences in performance, the phase durations for the treated and the non-treated eyes were then normalised to each observer's mean phase duration measured in the baseline condition with no prior monocular treatment[3], for the corresponding three-minute time window (bin) to account for any potential prolonged effects of experiencing binocular rivalry over time (see Klink et al., 2010). The distributions of

[2]Originally in a pilot study a prism that displaced one eye's image vertically by 6 dioptres was used to minimise the mismatch between the two eyes' inputs in luminance and contrast. However, preliminary testing suggested that the two eyes' images, even though there was a substantial vertical disparity, could still be fused by some observers (stereo vision was preserved as assessed by the TNO test), after wearing it for 20 minutes. Similarly, we attempted to use a size lens to magnify one eye's image by 9% to prevent fusion, but binocular fusion was also possible in some individuals. For that reason the inverting prism was chosen instead, as binocular fusion could never be achieved.

[3]The mean baseline duration was calculated from the durations pooled across both eyes/orientations and all repeated testing sessions.

these normalised phase durations were then plotted in the form of probability density functions (PDFs; bin size: 0.2), and the corresponding cumulative density functions (CDFs) were then fitted[4].

6.2.2 Results

Figure 6.1 shows the distributions of normalised exclusive phase durations for the stimulus presented to the treated eye (blue) and the non-treated eye (orange), after 2.5 hours of monocular treatment with an opaque patch, a Ganzfeld lens, or an inverting prism for a representative observer (S8). Only the durations measured during the first, the second and the last three-minute windows are plotted for the sake of simplicity. The distribution of the normalised baseline durations (black) for the corresponding time window is also shown in each plot. By visually inspecting Figure 6.1, for the first six minutes after the patch[5] was removed, there were more longer durations and fewer shorter durations for the stimulus presented to the previously treated eye, relative to the pre-treatment baseline durations. The opposite was found for the phase durations of the stimulus presented to the non-treated eye, whereby the distribution became more skewed to shorter durations. In this sense, the relative dominance between the eyes has been shifted in favour of the previously treated eye after monocular treatment. When tested 30 minutes after the patch was removed, the exclusive phase durations experienced by the two eyes became similar to those measured in the baseline condition, indicating a decay over time of the effects induced by monocular treatment. It is important to note that these patterns of results were revealed with all three types of monocular treatment. When pooled

[4]For the details of the fitting procedures, see Chapter 2, Section 2.4.

[5]The term "patch" is hereby used to refer to the opaque patch, Ganzfeld lens, or inverting prism.

across all the subjects tested, the group data exhibited similar patterns (not shown).

To quantify the effect produced by the opaque eye patch, the Ganzfeld lens, and the inverting prism, the ratio of mean exclusive phase duration experienced by the treated eye to that for the non-treated eye of each individual as a function of time following the end of monocular treatment (binned every three minutes) is plotted in Figure 6.2a. To reiterate, these data are collated across the left and right eyes and the horizontal and vertical orientations, such that the computed ratio cannot be explained by any existing biases in the sensitivity of the eye or orientation prior to monocular treatment. Therefore a ratio above unity indicates an enhanced dominance of the treated eye relative to the other eye following the treatment (note that a ratio of one does not mean a perfect balance between the two eyes but no change in eye dominance after treatment). In general, a shift in eye dominance towards the treated eye can be seen for all types of monocular treatment, which was largest immediately after the patch was removed. These changes were also confirmed by the results of permutation tests, which compared the mean or median phase durations between the treated and non-treated eyes in each type of monocular treatment for each individual[6] (see Table 6.1). Moreover, these effects declined rapidly within the first 12 minutes and then gradually reached a plateau, and this pattern of results is evident in all subjects tested[7] (see Figure 6.3a for group average

[6]For the post-patching measurements, the raw durations were permuted between the individual's eyes, and the difference in mean/median permuted durations between the two eyes was obtained. After repeating this procedure 10000 times, a p value evaluating whether the two eyes' measures were significantly different was computed as the proportion of times when the difference (absolute value) calculated from the permuted data was greater than that using the original data.

[7]Whilst the ratio returned to a level at which the treated and the non-treated eyes did not differ (indicated by the dashed line) towards the end of the 30-minute testing session for some individuals, the effects seemed to last longer for others.

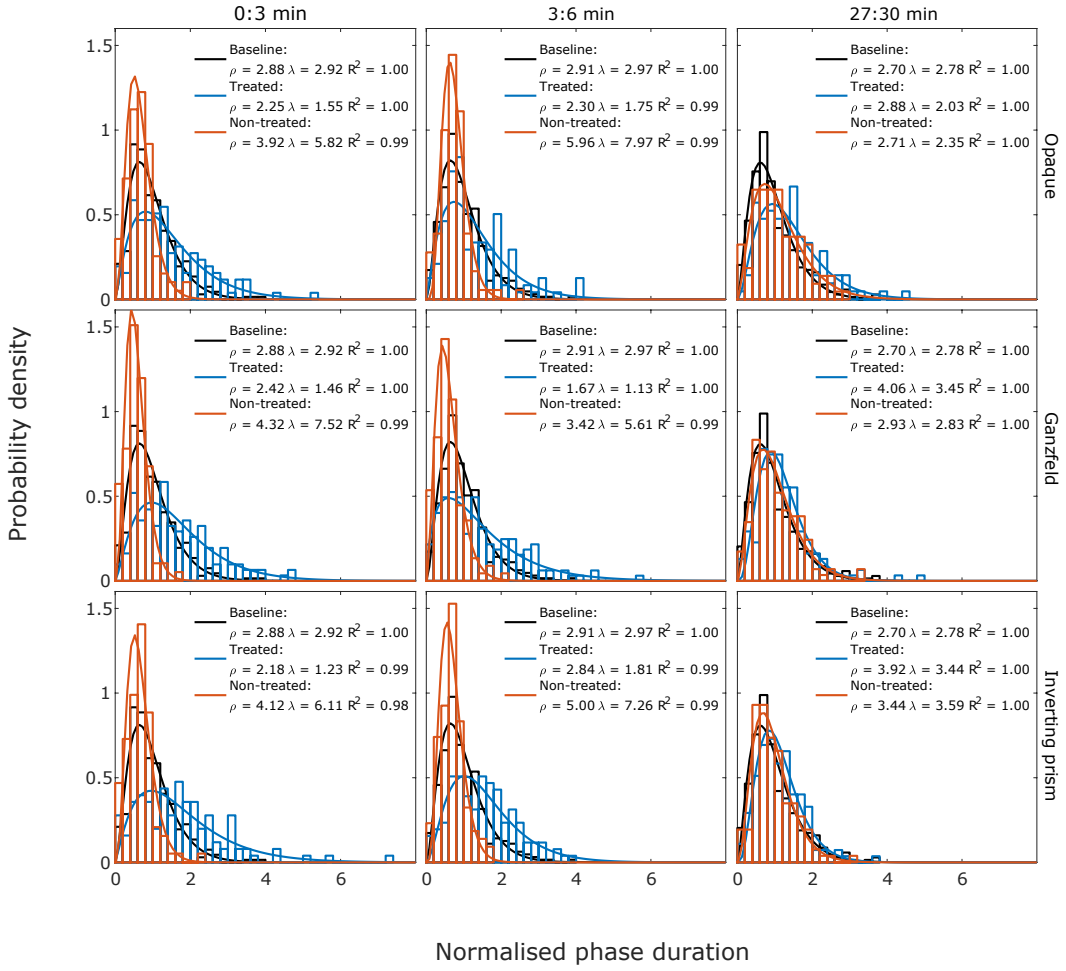
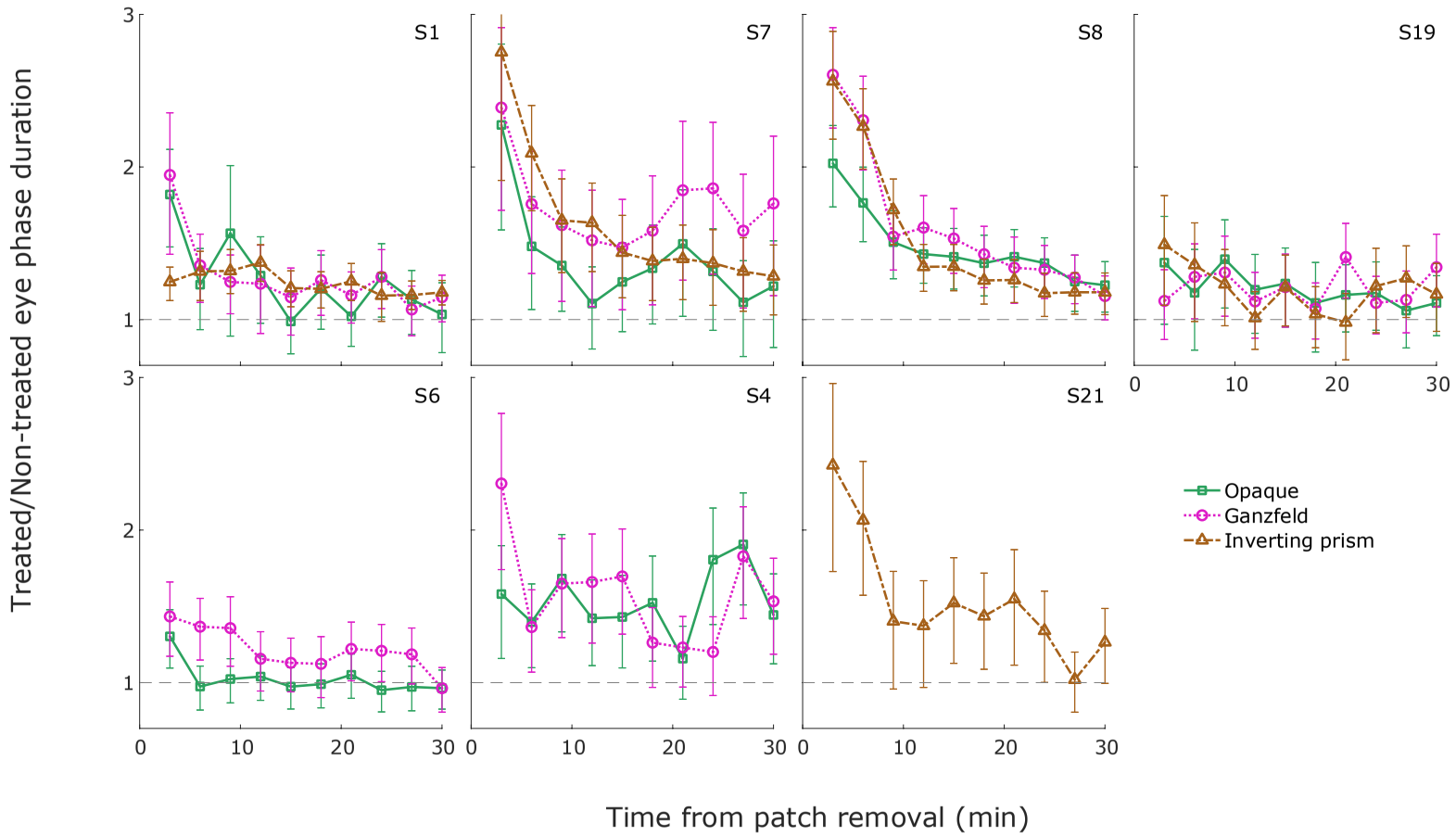


Figure 6.1: Distributions, plotted as probability density functions, for normalised exclusive phase durations experienced by S8 in Experiment 6. Each row corresponds to a treatment condition (i.e. opaque patch, Ganzfeld lens, or inverting prism) and each column corresponds to a time window (0–3, 3–6 and 27–30 minutes) within which the phase durations were pooled. Separate distributions for the stimulus presented to the previously treated eye (blue), and that for the non-treated eye (orange) are shown. Also plotted in each graph are the distributions for the pre-treatment (i.e. baseline) measurements (black). The curves are plotted as gamma PDFs, with the parameters estimated from the gamma fits of CDFs (Equation 2.5; see Chapter 2, Section 2.4). The fit results, including the estimated parameters, ρ and λ, and the goodness of fit indicated by R^2 are shown for each plot.

results). Similar results were obtained when the effect was assessed based on the percentage of time in total the treated eye's image was exclusively perceived (i.e. predominance) compared to that for the non-treated eye, which are demonstrated in Figure 6.2b and Figure 6.3b for individual and group average data, respectively. As phase duration and predominance are mathematically independent, the agreement in the results between the two metrics of treatment effect confirmed that our findings are robust and reliable. Overall, the observed pattern of time course of these effects replicated Lunghi et al.'s (2013) findings (see Figure 1.25).


S1
S7
S8
S19
S6
S4
S21
Opaque
Ganzfeld
Inverting prism
Treated/Non-treated eye phase duration
Time from patch removal (min)
1
2
3
0
10
20
30

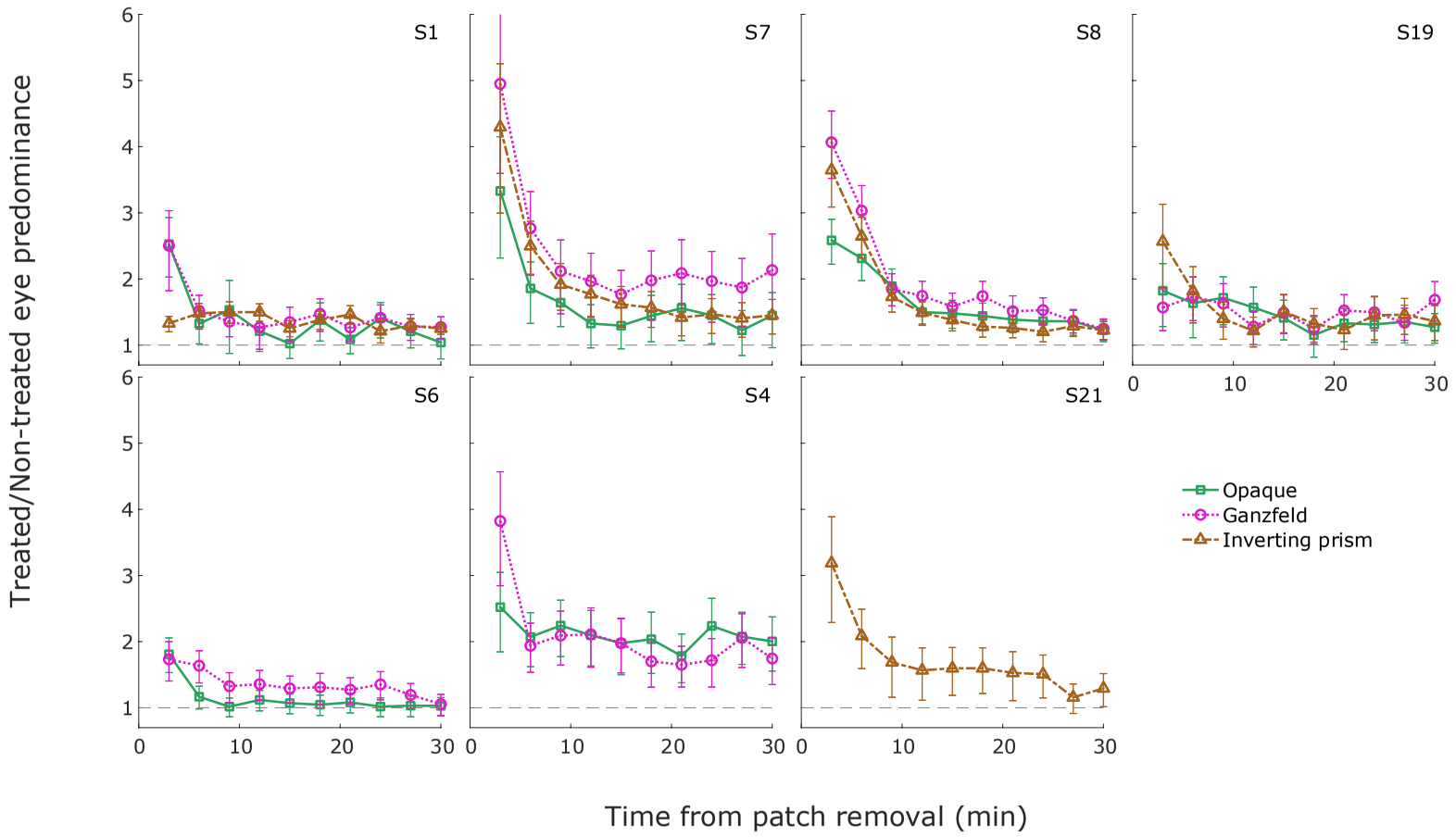

S1
S7
S8
S19
S6
S4
S21
Opaque
Ganzfeld
Inverting prism
Treated/Non-treated eye predominance
Time from patch removal (min)

Figure 6.2 *(previous page)*: The time course of the relative eye dominance following monocular treatment for each individual in Experiment 6. Symbols and colours indicate the treatment condition (i.e. opaque patch, Ganzfeld patch, or inverting prism). (a) The ratio of mean exclusive phase duration experienced by the treated eye to that for the non-treated eye as a function of the time elapsed since removing the patch. The dashed horizontal line signifies an independence of mean phase duration on whether the stimulus was presented to the previously treated or non-treated eye. (b) Same as (a) but in terms of stimulus predominance. Error bars are bootstrapped 95% confidence intervals (10000 repetitions).

The changes in sensory eye dominance can also be clearly seen from the average results for all participants (Figure 6.3). The time course of the effect, indicated by the ratio of the mean exclusive phase duration or predominance for the treated eye to that for the non-treated eye can be fitted by an exponential decay function using Equation 2.6 with three free parameters (a, τ, b; for fitting procedures see Chapter 2, Section 2.4).

Permutation tests were performed to compare the effects produced by different types of monocular treatment (3 pairwise comparisons in total) at the group level, in terms of the estimated parameters from the curve fits[8]. Specifically, the raw phase durations for each observer were randomly permuted across the two conditions to be compared. A ratio was then computed for every time bin for each observer based on the mean permuted durations for the two eyes. The mean ratio across observers was subsequently obtained for each time bin, and the resultant time course was fitted to using Equation 2.6. This procedure was repeated 10000 times. Consequently, a p value for the given pairwise comparison was obtained (computed from the permuted and the original data) for each parameter of the curve fits. As some participants did not complete all three treatment conditions, only the

[8]This analysis was only performed in terms of phase duration but not predominance as the number of observations for the latter was not sufficient to conduct permutations.

Table 6.1: The p values obtained from permutation tests (number of permutations: 10000) that compared the mean or median exclusive phase durations experienced by the treated eye and the non-treated eye in the three types of monocular treatment for each observer, measured at 0–3 or 27–30 minutes after removing the monocular treatment.

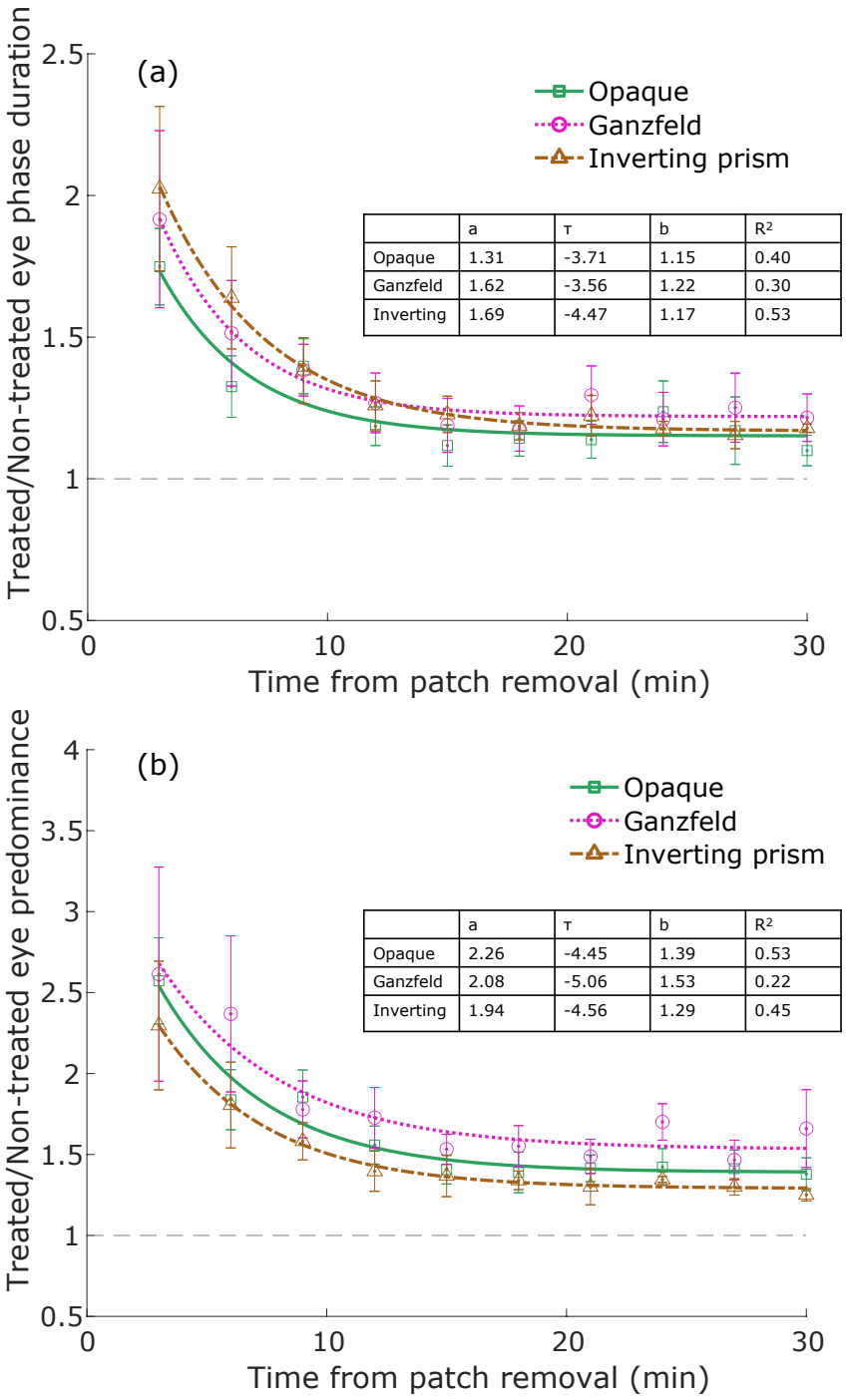
Observer	Opaque		Ganzfeld		Inverting	
	t_{0-3}	t_{27-30}	t_{0-3}	t_{27-30}	t_{0-3}	t_{27-30}
			Mean			
S1	$< .001$	.065	$< .001$	.863	$< .001$	$< .001$
S7	$< .001$	.904	$< .001$	.023	$< .001$	.094
S8	$< .001$	.003	$< .001$	.026	$< .001$	.015
S19	.003	.405	.507	.034	.057	.255
S6	$< .001$	.294	.006	.834	-	-
S4	.015	.085	$< .001$	.024	-	-
S21	-	-	-	-	$< .001$	.111
			Median			
S1	$< .001$	.673	$< .001$	.234	$< .001$	.001
S7	.025	.591	$< .001$	.031	$< .001$	.389
S8	$< .001$	.026	$< .001$	.022	$< .001$	.014
S19	$< .060$	.674	.068	.888	.297	.035
S6	.004	.729	.230	.704	-	-
S4	.006	.342	$< .001$	.087	-	-
S21	-	-	-	-	$< .001$	.117

data from observers who completed both conditions in a given pair to be compared were included for this analysis. The results are summarised in Table 6.2, which indicated that none of the comparisons differed significantly with respect to any of the three parameters (corrected for multiple comparisons using the Holm-Bonferroni method as proposed by Holm (1979)).

Table 6.2: The results of permutation tests (number of permutations: 10000), in p values, for three pairwise comparisons between different types of monocular treatment in terms of the estimated parameters, a, τ, and b from the curve fits of the time courses shown in Figure 6.3.

	Opaque-Ganzfeld			Opaque-Inverting			Ganzfeld-Inverting		
	a	τ	b	a	τ	b	a	τ	b
p	.596	.924	.080	.901	.580	.625	.399	.255	.190

In summary, the results show that covering one eye for 2.5 hours with an opaque patch, a Ganzfeld lens, or an inverting prism produced similar effects on binocular rivalry dynamics. The previously treated eye was strengthened relative to the other eye—the image viewed by this eye was exclusively perceived both for longer periods and for more time in total following the treatment. Importantly, the type of visual information which the eye was deprived of was different for the three treatment conditions. The opaque patch removed all information whilst the Ganzfeld lens only eliminated spatial content. The inverting prism, by contrast, prevented binocular fusion but both luminance and contrast information were preserved in the treated eye, matching that in the other eye. The finding that the magnitude and time course of this phenomenon were comparable for the three types of monocular treatment, therefore, implies that neither the lack of luminance nor contrast, in one eye, is a necessary requirement for the shift in sensory eye dominance produced by short-term monocular deprivation. In addition,



	a	τ	b	R^2
Opaque	1.31	-3.71	1.15	0.40
Ganzfeld	1.62	-3.56	1.22	0.30
Inverting	1.69	-4.47	1.17	0.53

	a	τ	b	R^2
Opaque	2.26	-4.45	1.39	0.53
Ganzfeld	2.08	-5.06	1.53	0.22
Inverting	1.94	-4.56	1.29	0.45

Figure 6.3: The same as Figure 6.2 except that the data are averaged across all observers. Error bars represent ±1 SEM between individuals. The time course for each treatment condition was fitted with an exponential decay function (Equation 2.6). The estimated parameters and R^2 of the fits are also shown. (a) The ratio of mean exclusive phase duration for the treated eye to that for the non-treated eye. (b) Same as (a) but calculated using stimulus predominance.

the similar time course of the effects produced by opaque patching compared to those resulting from the other types of treatment confirmed that dark adaptation (which occurs when the eye is fully occluded) in itself may not be the principal contributing factor producing shifts in eye dominance.

6.3 Experiment 7: What is happening to sensory eye dominance during monocular inversion?

The shifts in sensory eye dominance observed in both the current and previous studies were measured at the point when monocular treatment has been terminated, but it is interesting to investigate the visual processes taking place during the adaptation period, to see how these changes build up throughout the course of monocular treatment. Indeed, Begum and Tso (2016) have demonstrated in adult macaques that physiological changes of V1 neurons occurred during monocular deprivation in that the responsiveness of the non-deprived eye gradually decreased. These changes started to decline once the deprivation was terminated. These results suggest that shifts in ocular dominance may not simply be a rebound effect taking place once the deprived eye is re-exposed to normal visual input. However, the complementary behavioural evidence is yet to be obtained.

With both the opaque patch or the Ganzfeld lens, it is impossible to measure sensory eye dominance behaviourally without removing the occluder from the patched eye. This limitation can be overcome however by using the inverting prism, as the treated eye is still stimulated with spatial information to allow the measurement of perception during binocular rivalry.

In this experiment, therefore, sensory eye dominance was measured with the BR task used in Experiment 6, at several time points during monocular treatment with the inverting prism.

6.3.1 Methods

Six participants, including five (S1, S7, S8, S19, and S21) that took part in Experiment 6 and another observer (S9), participated in Experiment 7. The apparatus and stimuli for the BR task were identical to those used in Experiment 6.

The procedure was identical to that for the prism condition in Experiment 6, with the exception of the time point when BR was measured. Participants performed the BR task immediately after the onset of the inverting prism, and subsequently every 30 minutes, until the end of the 150-minute adaptation period, yielding six measurements for each observer. The prism was then removed and BR was measured again, immediately, and at 30 minutes following the prism removal. For two observers (S19 and S21), the monocular treatment only lasted 60 minutes[9], leading to three measurements of BR during the adaptation period. Each measurement lasted 3 minutes. As in Experiment 6 the procedure was repeated at least twice for each eye.

The data were treated and analysed in the same manner as in Experiment 6, with the exception that the exclusive phase durations were normalised to the mean baseline durations pooled over only the first three-minute time window. This is because BR was not measured continuously for 30 minutes in this experiment, but in three-minute trials separated in

[9]This was due to unavailability of these two participants. Nevertheless they were measured after all other participants had completed the testing, and the results showed that most people reliably exhibited shifts in eye dominance following 30-minute treatment.

time.

6.4 Results

The distributions of normalised exclusive phase durations for a representative observer (S8) are illustrated in Figure 6.4. Each subplot depicts the durations pooled over a three-minute trial, separately for the treated eye and the non-treated eye. For the measurements taken during the adaptation period, only the data for the first, the second, and the last measurement window are shown. The distributions for baseline phase durations (in the absence of monocular treatment) measured in Experiment 6 are also plotted (black). The phase duration distributions for the treated eye and the non-treated eye of this observer largely overlapped for those measured at the initial onset of monocular inversion, which were comparable to that for the baseline durations. By contrast, an alteration of the relative eye dominance, that increased probability of longer durations for the treated eye (blue) and shorter durations for the non-treated eye (orange), was revealed as soon as 30 minutes following the onset of wearing the prism. This pattern of results remained evident until the end of the monocular inversion period (i.e. 150 minutes after the onset), and was also the case immediately after removing the inverting prism (yellow: treated eye; purple: non-treated eye). Finally, the phase duration distributions for the two eyes became similar when measured 30 minutes after removing the prism, indicating a diminution of the effects. Although these are typical characteristics of the results found, there are some variations between individuals, which are detailed below.

The treatment effect for each individual, quantified by the ratio of mean exclusive phase duration for the treated eye to that for the non-treated

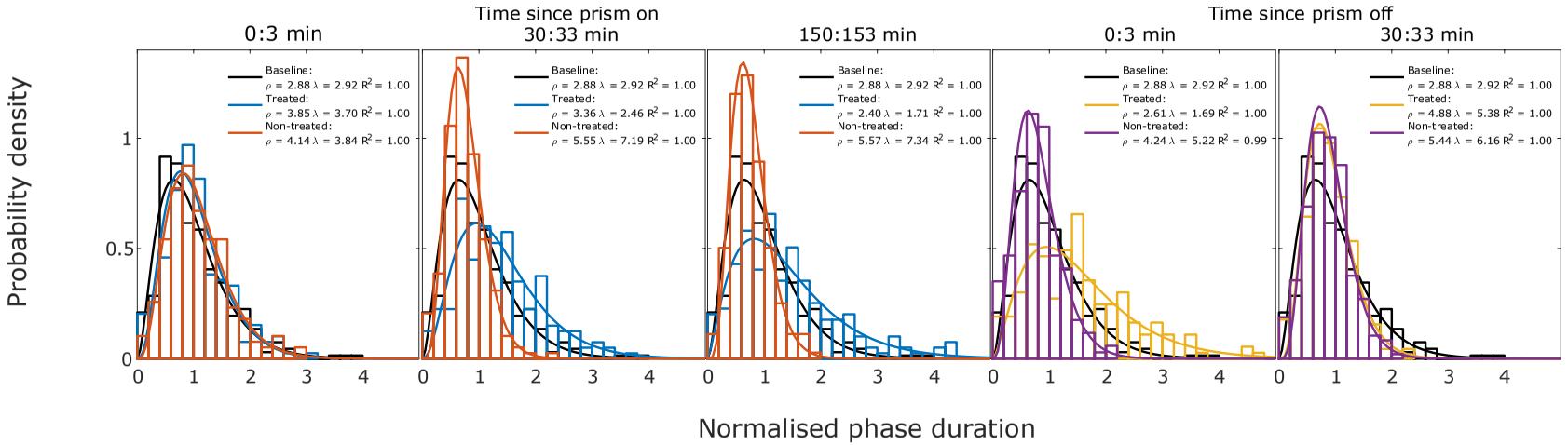
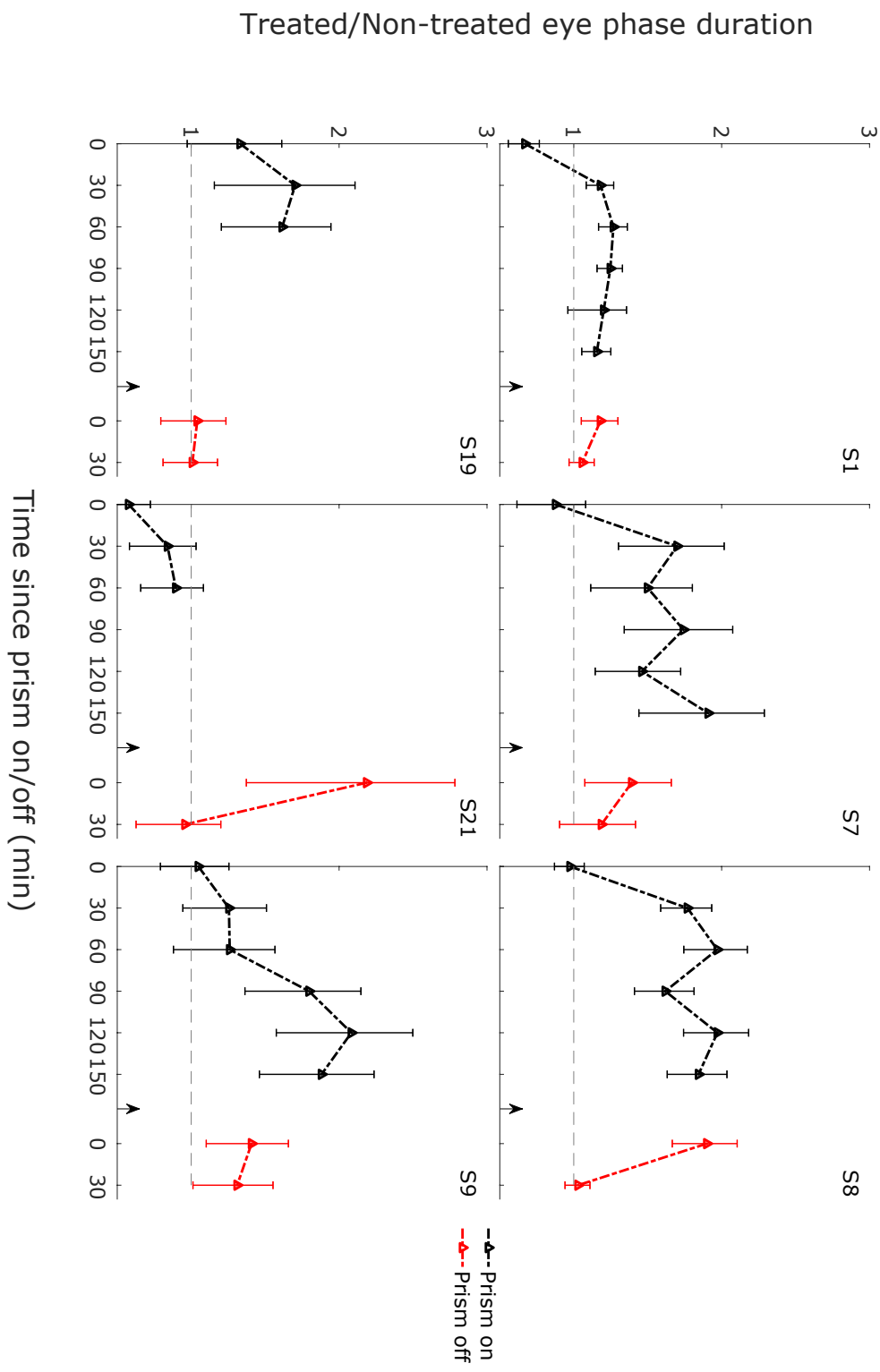


Figure 6.4: Probability density function of normalised exclusive phase durations for S8 in Experiment 7. Each subplot represents the durations within a three-minute time window as indicated at the top. The three leftmost subplots are the durations measured during the monocular inversion period (blue: treated eye; orange: non-treated eye), whereas the data plotted in the two rightmost subplots were measured after the prism was removed (yellow: treated eye; purple: non-treated eye). Other aspects of the plots are the same as in Figure 6.1.

eye, as a function of time elapsed from the onset/offset of the monocular treatment with the inverting prism, is demonstrated in Figure 6.5a. It can be seen that the most apparent discrepancy between individuals lay in the effect observed at the prism onset (0 minute). For three observers (S7, S8 and S9), the ratio at this point was not different from unity which indicates the independence of eye dominance on whether the eye underwent monocular inversion. For another two observers (S1 and S21), however, a ratio marginally lower than one was the case. This indicates a reduced dominance of the treated eye relative to the other eye immediately after the onset of monocular inversion for these observers. This is somewhat conceivable, as the upright image might have gained dominance over the inverted image at the initial stage of the monocular treatment because of its higher behavioural relevance (see Section 6.5). It should not be overlooked, however, that the orientation of the grating stimulus appeared identical when viewed with and without the prism. The prism only affected the appearance of the scene in the background environment (e.g. the monitor, the desk) which was dimly lit. For the other observer (S19), the expected enhancement of the treated eye's dominance, was observed as early as the onset of the monocular inversion.


Treated/Non-treated eye phase duration
S1
S19
S7
S21
S8
S9
Prism on
Prism off
Time since prism on/off (min)

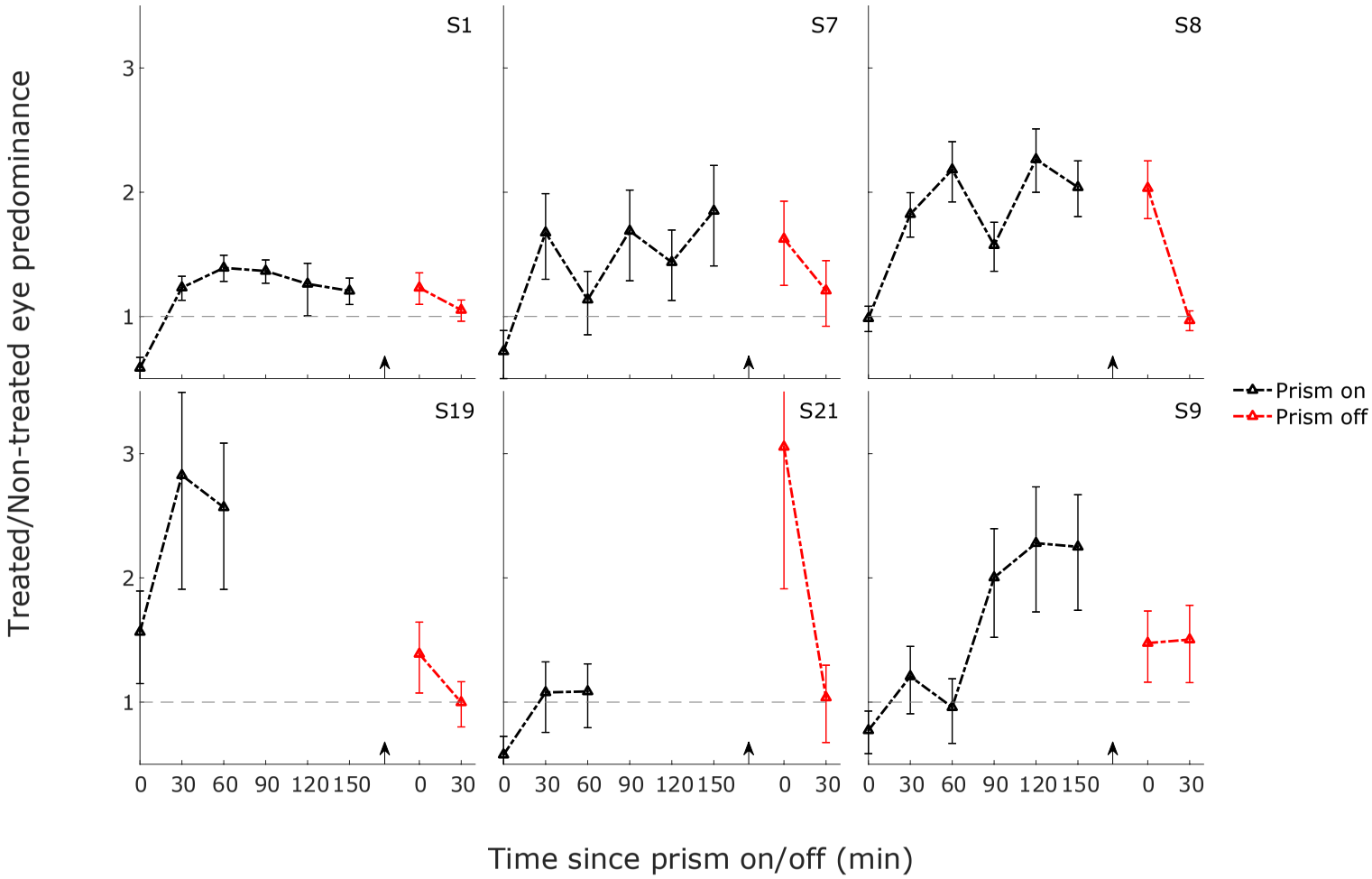

S1
S7
S8
S19
S21
S9
Prism on
Prism off
Treated/Non-treated eye predominance
Time since prism on/off (min)
1
2
3
0 30 60 90 120 150 0 30

Figure 6.5 *(previous page)*: The time course of the relative eye dominance following the onset/offset of monocular inversion for each individual in Experiment 7. The black symbols and lines are for the data measured during the monocular inversion period whereas the data measured after removing the prism are in red. (a) The ratio of the mean exclusive phase duration experienced by the treated eye to that for the non-treated eye as a function of the time elapsed since putting on or off the prism. The arrow marks the point at which the inverting prism was removed. The dashed line indicates an independence of mean phase duration on whether the stimulus was presented to the treated or non-treated eye. (b) Same as (a) but in terms of stimulus predominance. Error bars are bootstrapped 95% confidence intervals (10000 repetitions).

At 30 minutes after the onset of monocular inversion, all but one subject exhibited increased dominance for the treated eye compared to the non-treated eye, as indicated by the ratios greater than one. This monocular inversion effect seemed to saturate at this point for S1, S7, S8 and S19, and at 90 minutes following the prism onset for S9. The other observer, S21, showed increased relative dominance of the treated eye subsequently compared to the first measurement after viewing through the prism, although the non-treated eye was still slightly more dominant. It is possible that a bias towards the treated eye may have been observed if monocular inversion was continued for this participant, although their limited time availability for testing prevented this from being explored.

Sensory eye dominance after removing the inverting prism was also assessed. As shown in Figure 6.5a, there was a clear dominance in phase duration for the stimulus presented to the eye that viewed the inverted image. This bias diminished, when it was examined 30 minutes later. Similar results were found when eye dominance was computed with respect to stimulus predominance (Figure 6.5b). The results replicate the findings of Experiment 6, confirming that the shifts in eye dominance produced by the

inverting prism are reliable.

In summary, these results demonstrated that the effect of monocular inversion on sensory eye dominance became measurable as early as 30 minutes following introduction of the prism. The changes in eye dominance occurred without a need for re-exposure to normal binocular viewing conditions, consistent with Begum and Tso's (2016) finding in macaques that the non-deprived eye's responsiveness gradually reduced during the monocular deprivation period. These observations make the account based on a rebound effect of the treated eye less likely, as the onset of the changes in eye dominance seems not to depend on the termination of monocular treatment.

6.5 Discussion

The influence of short-term monocular deprivation on inter-ocular balance has recently been demonstrated in several studies by showing increased relative contributions from the deprived eye on a range of binocular tasks (e.g. Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). However, the mechanism driving this phenomenon remains elusive. This issue was addressed in the current chapter by comparing changes in BR dynamics as a consequence of three types of monocular manipulation. Crucially, the results suggest that the changes in sensory eye dominance are possibly driven by mechanisms in response to imbalanced processing between the two eyes, arising from inter-ocular differences in both low-level sensory input and higher-level cognitive processes during the monocular treatment period. In addition, it has also been shown that the effect developed relatively quickly, after only 30 minutes of treatment, not showing a further accumulation effect in magnitude with continuation of the monocular treatment period.

The three types of monocular treatment rendered a distinct distortion of visual input in the treated eye, despite similar consequences on sensory eye dominance. Specifically, the opaque and Ganzfeld patching both degrade the visual information in the patched eye, which may result in the operation of a compensatory mechanism to rebalance the neuronal activity associated with the two eyes. In the case of the inverting prism, an imbalance between the two eyes' processing may also be present, which plausibly results from selective deployment of top-down attention to one eye over the other.

It is worth noting that the disruption of binocular fusion in the prism condition presumably gives rise to rivalry between the two eyes. Interestingly, some of our participants reported being able to ignore the inverted image in the treated eye after wearing the prism for some time. This is possibly because the information from the upright image is more useful (biologically relevant) compared to the inverted image. Dieter and Tadin (2011) proposed that the degree of attentional control over binocular rivalry dynamics is likely to increase with the difference in behavioural relevance between the two eyes' images[10]. Supporting this notion, an emerging body of evidence suggests that stimulus predominance during binocular rivalry can be modulated by higher-level cognitive and social factors, other than elementary visual properties (e.g. Alpers & Pauli, 2006; Anderson, Siegel, & Barrett, 2011; Bannerman, Milders, De Gelder, & Sahraie, 2008; Chong et al., 2005; Engel, 1956; Goryo, 1969; LoSciuto & Hartley, 1963; Mudrik, Deouell, & Lamy, 2011; Yu & Blake, 1992), presumably through increased attention to one eye's stimulus because of its superior relevance to the other stimulus. In particular, a stimulus created through inversion of faces or other real-life images, resembling that produced by the inverting prism, has

[10]For example, one eye's stimulus is more behaviourally relevant than the other eye's while a task is performed that requires specific attention to the former but not the latter.

been shown to be less predominant than an upright image viewed by the other eye during binocular rivalry (Bannerman et al., 2008; Engel, 1956; Yu & Blake, 1992). This reinforces the possibility that in the prism condition the inverted image was suppressed for more time (and probably to a greater extent) than the upright image viewed by the non-treated eye when they underwent rivalry, leading to an imbalance in the visual processing associated with the two eyes. Consistent with the account that this form of inter-ocular imbalance has driven the effects found in the prism condition, Kim et al. (2017) have demonstrated increased dominance of an eye after it has undergone inter-ocular suppression evoked by conditions of CFS. Similar to the prism condition, the suppressed eye in that case was not deprived of sensory input other than the lack of awareness, but the directional changes in eye dominance still arose subsequently, possibly due to the compromised processing as a result of inter-ocular suppression.

It is reasonable to expect that the speculative attentional eye selection, in endogenous form, is even larger in the current prism condition than that found in laboratory-induced binocular rivalry, for example, between upright and inverted images. This is because the subject was allowed to perform normal everyday activities while wearing the prism, in which case the image orientation is highly relevant. Moreover, as the activities conducted were not controlled, the variation in the degree of selective attention deployed for completing these tasks[11] across the participants may partially explain the individual differences in the magnitude of effect observed in this condition. Further research may address this issue by manipulating the level of attentional demand during monocular treatment.

[11]For example, if the participant was reading a book, it considerably relied on the appropriate use of the upright image. By contrast, if the participant was simply staring at a wall, it did not matter whether the upright or the inverted image was perceived.

It is noteworthy that the phase scrambling of one eye's image adopted in some work (Bai et al., 2017; Zhou et al., 2014) may resemble the case of the inverting prism. In that condition, binocular fusion was prevented but sensory input may be considered balanced between the two eyes in the sense that the Fourier amplitude spectra were matched. The inter-ocular imbalance may have arisen from a bias in attending to the eye's image that was normal, as opposed to the phase-scrambled image. Nevertheless, it is also possible that the distortion of form information in the phase-scrambled image, may have contributed to the subsequent changes in eye dominance via a low-level mechanism. Thus, the present findings using the prism, where the contour information in the treated eye was preserved (though inverted), are novel and strongly support a role for higher-level contribution to sensory eye dominance plasticity.

There may be an alternative explanation, however, other than the introduction of inter-ocular imbalance. That is, the changes in eye dominance could be the consequence of interrupting binocular fusion. Nevertheless, this account seems unlikely for the following reason. A noteworthy aspect of the observed effect is the direction specificity—it was the treated eye, rather than the non-treated eye, that became more dominant. Such a consistent result would not be expected if the mere elimination of fusion drove the effect. This is in contrast to the findings of Bao, Dong, Liu, Engel, and Jiang (2018) where binocular fusion training improved inter-ocular balance measured with a range of binocular tasks (e.g. binocular rivalry, binocular phase combination). During the training period, their participants were exposed to viewing conditions in which some portions of the images viewed by the two eyes were blurred. The locations of these blurred patches were in compensatory positions in the two eyes, such that the participant needed

to combine the two eyes' images in order to see the full image (see Figure 6.6 for an example). During such training the two eyes had not only (roughly) balanced low-level sensory input, but also comparable attentional resource—no directional inter-ocular imbalance was introduced. Therefore the direction of changes in an eye depends on whether the eye is the dominant or the less dominant eye before training[12], but in the current study this depends on which eye has been treated.

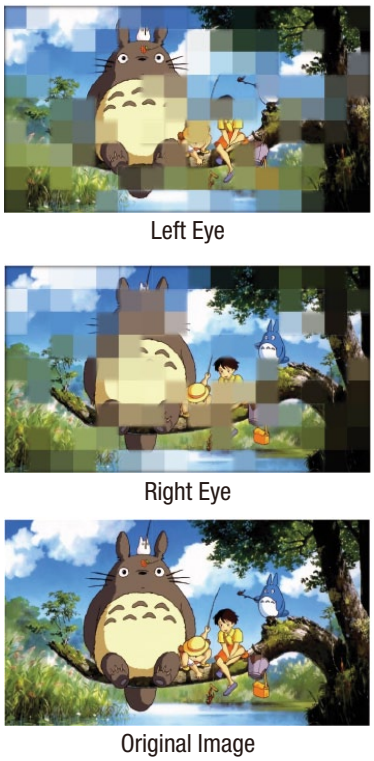


Figure 6.6: An illustration of the viewing conditions for the two eyes during binocular fusion training. Some portions of the left eye's image are blurred and some portions at non-corresponding positions of the right eye's image are also blurred. A focused full image can be formed by combining the two eyes' images. Adapted from Bao et al. (2018).

Furthermore, Bao et al. (2018) suggested that sensory eye dominance

[12]This is because in their study the result was a reduction in inter-ocular imbalance after training, by reducing the dominance of the dominant eye and increasing the dominance of the non-dominant eye, such that the pre-existing eye dominance dictated the effect.

may be subject to influences of multiple mechanisms of varying time scales. In the case of our results, however, the low- and higher-level processes appear to have similar time scales, indicated by the overlapping time courses of the three types of monocular treatment observed in Experiment 6. It is therefore reasonable to speculate that these low- and higher-level aspects of inter-ocular imbalance may act on a single mechanism, which in turn modulates the subsequent inter-ocular balance.

A plausible account is that inter-ocular imbalance existing in both low- and higher-level processing (produced by monocular treatment) modulates the apparent contrast of the two eyes' stimuli, such that the perceived contrast of the stimulus presented to the previously treated eye is strengthened. In other words, it is the contrast gain of each eye that is altered. However, this view is unsatisfactory for the following reasons. As indicated by the results of Experiment 5, the changes produced by short-term monocular deprivation relate to the strength of inter-ocular interactions, rather than the monocular gain of each eye. Moreover, it has been shown that monocular phase scrambling caused task-dependent results—changes in eye dominance were only observed with binocular rivalry but not binocular phase combination (Bai et al., 2017; Zhou et al., 2014). In addition, the patching effect revealed with cross-orientation dichoptic masking was not a good predictor of that measured with dichoptic masking between identical orientations across individuals (see Figure 1.28; Baldwin & Hess, 2018). If the contrast gain of each eye was altered, the same pattern of (and significantly correlated) results would be expected for different binocular tasks.

To summarise, this chapter has demonstrated the importance of inter-ocular imbalance, in triggering subsequent directional changes in sensory eye dominance, towards the presumably "disadvantaged" eye. This imbal-

ance may be with respect to low-level sensory input, higher-level cognitive processing, or a combination of both. One possibility is that the visual system operates on a compensatory mechanism to maintain balanced neuronal activity associated with the processing of the two eyes' inputs at a later stage (after the influence of higher-level processes), by regulating the strength of inter-ocular interactions.

Chapter 7

Experiment 8: Top-down and bottom-up contributions to the perceptual consequences of monocular deprivation[1]

7.1 Introduction

In the last chapter the possibility that higher-level attentional mechanisms modulate eye dominance plasticity was raised. As discussed in Chapter 1, Section 1.12, perceptual eye dominance during binocular rivalry is also subject to attentional modulation in that selective attention to one eye's stimulus increases its relative dominance over the other eye (e.g. Chong et al., 2005). Interestingly, Dieter, Melnick, and Tadin (2016) have demonstrated plasticity of attentional modulation of eye dominance—the degree

[1]The experiments described in this chapter have previously been published, in part, in abstract form [Wang, McGraw and Ledgeway, 2020b] and presented at the AVA Christmas Meeting, Cardiff, Cardiff University, December, 2019.

of attentional facilitation of an eye during BR was enhanced following training to selectively attend to this eye's image (Figure 7.1). In other words, their findings revealed an interaction between the effects of selective attention and attentional training on sensory eye dominance. Nonetheless, the form of plasticity shown in that study, namely perceptual learning, relies on training on specific visual tasks and the improvement in performance on these tasks is often shown to have little transferability (Levi & Polat, 1996; Polat, Ma-Naim, Belkin, & Sagi, 2004). Whilst potentially bridging attentional eye selection and eye dominance plasticity, its bearing on mechanisms underpinning effects of short-term monocular treatment remains unknown.

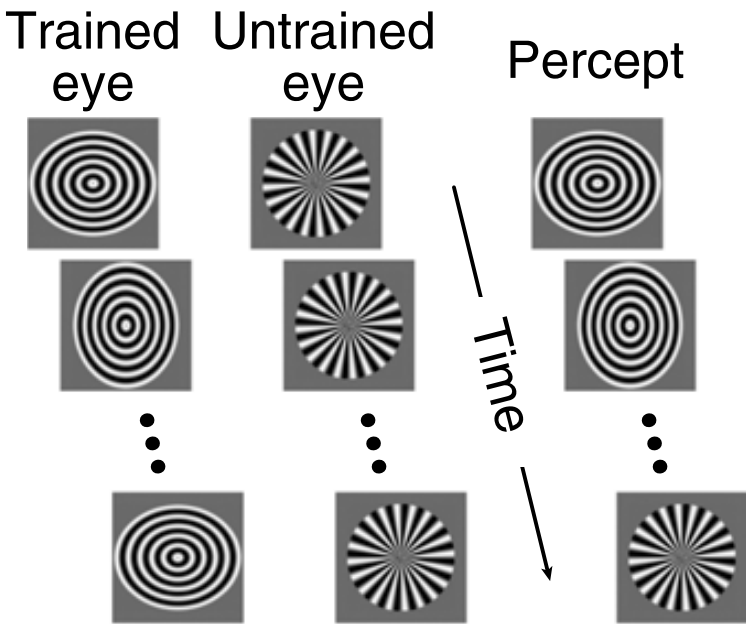


Figure 7.1: Training paradigm used by Dieter et al. (2016). A concentric grating was presented to one eye while a radial grating was presented to the other eye. The participant was instructed to track changes in the aspect ratio of the concentric grating, which required reliable selective attention to this stimulus whilst experiencing BR. The trained eye was kept constant throughout the training for each participant.

Before the role of higher-level attention in driving the subsequent changes

in eye dominance following monocular treatment can be explored, it is necessary to substantiate the instantaneous influence of attention on eye dominance measured using identical stimuli and protocols to those used for quantifying the effects of monocular treatment. This is because these two sources of potential attentional effects may confound with each other. Therefore the first aim of this chapter was to examine whether selectively attending to an eye's stimulus enhances its dominance during binocular rivalry. The second aim was to investigate if attentional selection interacts with the effect of monocular deprivation[2] on eye dominance.

There are several methods frequently used in experiments to direct top-down attention selectively to one of the two eyes. In some studies participants performed a task requiring reliable attention to one eye's stimulus but not the other (Chong & Blake, 2006; Chong et al., 2005; Dieter et al., 2016; Hancock & Andrews, 2007). For example, Chong et al. (2005) asked participants to count the frequency of changes in features (e.g. spatial frequency) of a named stimulus while the subjective percepts during BR were tracked. In other studies, the engagement of selective attention has relied on explicit attentional instructions (Meng & Tong, 2004; Mishra & Hillyard, 2009; Ooi & He, 1999; Zhang et al., 2012). Here a variant of the latter method was used: Participants were instructed to attend to either eye's stimulus, tagged with a named colour, and perceptual dominance during BR was measured by reporting the perceived orientation regardless of its colour.

[2]Thus the inverting prism used in the last chapter was not tested in the following experiments.

7.2 Experiment 8a

7.2.1 Methods

Five observers participated in this experiment (age range: 24–50 years, two females). Sensory eye dominance was quantified by measuring the perceptual dominance at onset binocular rivalry between red and green, orthogonal gratings. The attentional state of the observer was manipulated by either providing no instructions of selective attention (i.e. neutral condition), or requiring the participant to attend to one of the colours (i.e. red or green) which was tagged to a specific eye. For example, it was the right eye that was selectively attended to when the participant was asked to "attend to the red grating" which was presented to the right eye in a given block of trials. Meanwhile, perceptual dominance at the onset of binocular rivalry was measured whilst inter-ocular contrast difference was varied using the method of constant stimuli. Specifically, the contrasts of the two eyes' stimuli were varied from 0–40% in a "see-saw" manner, while the average was kept constant at 20%. That is, the relative contrast, calculated as the difference between the two eyes' contrasts (Michelson) divided by their sum, was varied from -1 to 1 in seven equal steps[3]. For a detailed description of apparatus, stimuli and tasks used in this experiment, see Chapter 2, Sections 2.2 and 2.3.4.

Two types of deprivation were examined, using an opaque patch or a translucent lens (i.e. Ganzfeld). The eye that was patched was randomly chosen for each observer and was kept consistent throughout the experiment. The measurement of perceptual eye dominance was completed both

[3]For example, 0% for the right eye's grating and 40% for the left eye's grating yielded a relative contrast of -1 with reference to the right eye.

before, and immediately after 30 minutes of monocular deprivation. This deprivation period was chosen on the basis of the findings of Experiment 7 which showed that the effect saturated after 30 minutes for most of the participants tested. Only one set of measurements that lasted approximately 5 minutes, was taken after every patching period, to avoid the waning of the effect over time. Therefore at least 6 measurements, including 3 attentional states[4] $\times$ 2 eye-colour configurations[5], were completed for each of the 3 patching conditions (i.e. baseline, opaque, and Ganzfeld patching), in a pseudorandom order. The data were collapsed across the two eye-colour configurations for each patching condition, yielding 3 attention conditions tested for at least 2 runs[6], which were neutral (i.e. no attentional instructions), attending to the patched eye, and attending to the non-patched eye[7]. A psychometric function showing how perceptual eye dominance depends on the relative contrasts of the stimuli was thereby generated for each attention condition for each observer. A curve was fitted to each observer's results using Equation 2.7 (for the details of fitting, see Chapter 2, Section 2.4).

7.2.2 Results

The psychometric functions for an example individual (S8) are illustrated in Figure 7.2. Each graph shows the data obtained in the three attention conditions for a given patching regime. As can be seen in the baseline con-

[4]That is, attending to the red grating, attending to the green grating, and no attentional instructions.

[5]That is, the red grating presented to the right eye and the green grating presented to the left eye, and the converse configuration.

[6]Whenever one of the eye-colour configurations for an attention condition was tested for more than one run, the other configuration was tested for the same number of runs, in order to counterbalance any extraneous bias in perceiving one of the colours.

[7]For the baseline condition, attending to the patched eye refers to attending to the eye that was to be patched, which was kept constant for each individual.

dition, when no attentional instructions were given (i.e. neutral condition), the likelihood that an eye's grating dominated perception on a trial was approximately equal for the two eyes at equivalent contrast (i.e. a relative contrast of zero on the abscissae). The psychometric function was shifted laterally, when an eye's grating was selectively attended to—the grating presented to this eye required less contrast for it to dominate perception. This effect of selective attention was revealed in all three patching conditions. Moreover, the results also showed that patching an eye shifted the psychometric function in favour of that eye, and the magnitude of the shifts was comparable for opaque and Ganzfeld patching. Crucially, in some cases the enhancement of the previously patched eye could be counteracted if participants were required to attend to the colour of the non-patched eye's grating. For example, the position of the dash-dot curve (and squares) in Figure 7.2b resembles that of the solid curve (and circles) in Figure 7.2a.

To examine the observed effects at the group level, the point of subjective equality (PSE) with respect to the patched eye relative contrast for each condition was averaged across all five subjects, and is shown in Figure 7.3. In general, there were distinct effects of the two attentional instructions (attending to the colour presented to the patched eye and attending to the colour presented to the non-patched eye) on the PSE. That is, attending to the previously patched eye decreased the PSE relative to that measured in the neutral condition whereas attending to the non-patched eye increased it. In addition, there was an overall shift of the PSEs for all three attentional states with monocular patching (either opaque or Ganzfeld) compared to the baseline measurement, such that the patched eye's grating required less contrast for equal perceptual dominance of the two gratings (i.e. a downward shift in Figure 7.3). A 3×3 two-way ANOVA

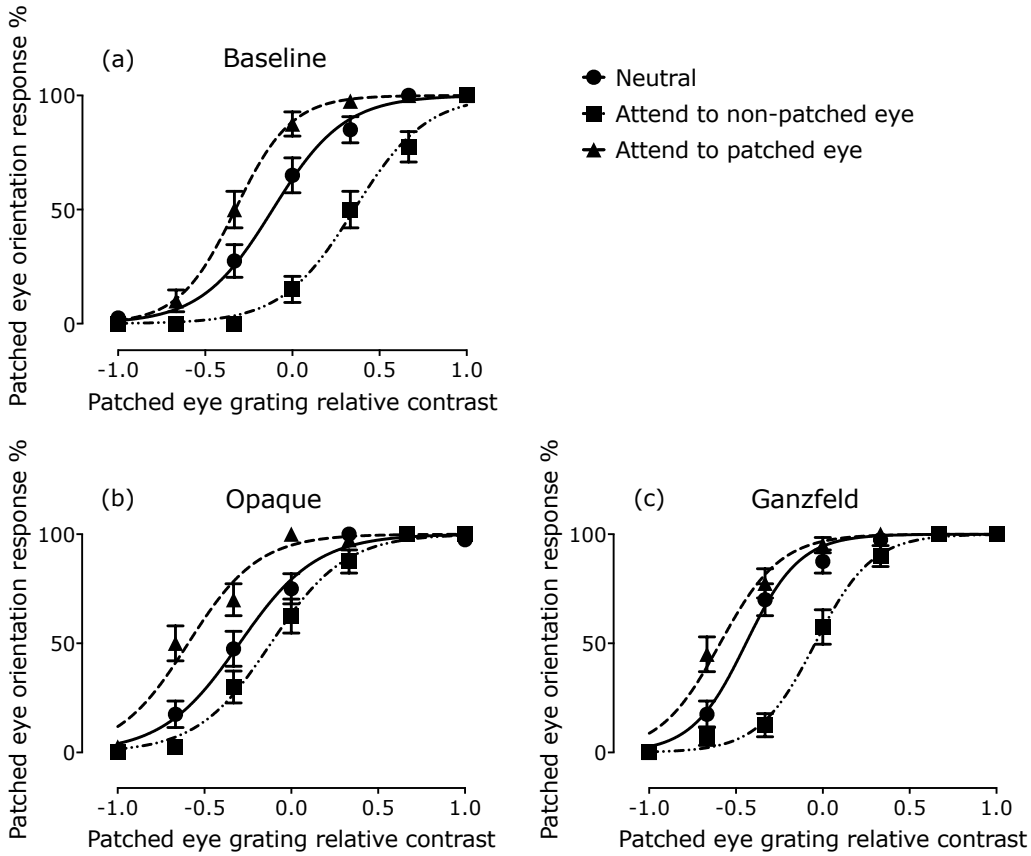


Figure 7.2: Psychometric functions of perceptual eye dominance measured in the neutral, attending to the patched eye, or attending to the non-patched eye conditions, for one participant (S8) in Experiment 8a. The abscissa indicates the relative contrast of the grating presented to the patched eye, ranging from -1 which means no contrast, to 1 where it had maximum contrast (for more details of this metric please refer to Chapter 2, Section 2.2). The ordinate is the percentage of trials on which the patched eye's grating was reported dominant. The error bars represent ± 1 standard error of the percentage. These data were obtained (a) in the absence of monocular patching (baseline), or following 30-minute of monocular patching with (b) an opaque patch or (c) a Ganzfeld lens.

revealed significant main effects of *attention* ($F_{(2,8)} = 16.79, p = .001$) and *patching* ($F_{(2,8)} = 25.74, p < .001$). However, the interaction between these two factors was not significant ($F_{(4,16)} = .454, p = .768$). The results of post-hoc, paired-samples t-tests[8] indicated that the difference between every pair of attention conditions was significant (neutral vs. attending to the patched eye: $t = -3.77, p_{holm} = .04$; neutral vs. attending to the non-patched eye: $t = 3.94, p_{holm} = .04$; attending to the patched eye vs. attending to the non-patched eye: $t = 4.22, p_{holm} = .04$). Moreover, the PSE measured after monocular deprivation with either the opaque patch or the Ganzfeld lens significantly differed from that measured in the baseline condition (opaque vs. baseline: $t = 4.92, p_{holm} = .016$; Ganzfeld vs. baseline: $t = 6.03, p_{holm} = .011$). The difference between the two monocular deprivation conditions (opaque vs. Ganzfeld patching) was however not significant ($t = -2.46, p_{holm} = .07$). In addition to PSE, we also assessed whether our experimental conditions have led to systematic changes in slope of the psychometric functions. However, the results of ANOVA showed that monocular patching ($F_{(2,8)} = 3.39, p = .086$) or attentional instructions ($F_{(2,8)} = .995, p = .411$) did not influence the slope significantly, nor did their interaction ($F_{(4,16)} = .505, p = .733$).

7.3 Experiment 8b

In Experiment 8a, the effect of monocular deprivation for only one randomly chosen eye of the observer was examined. To further test the generality of the conclusion that monocular deprivation and attentional eye selection can independently modulate eye dominance during BR, the effect of patching

[8]The reported p values were corrected for multiple comparisons using the Holm-Bonferroni method as proposed by Holm (1979).

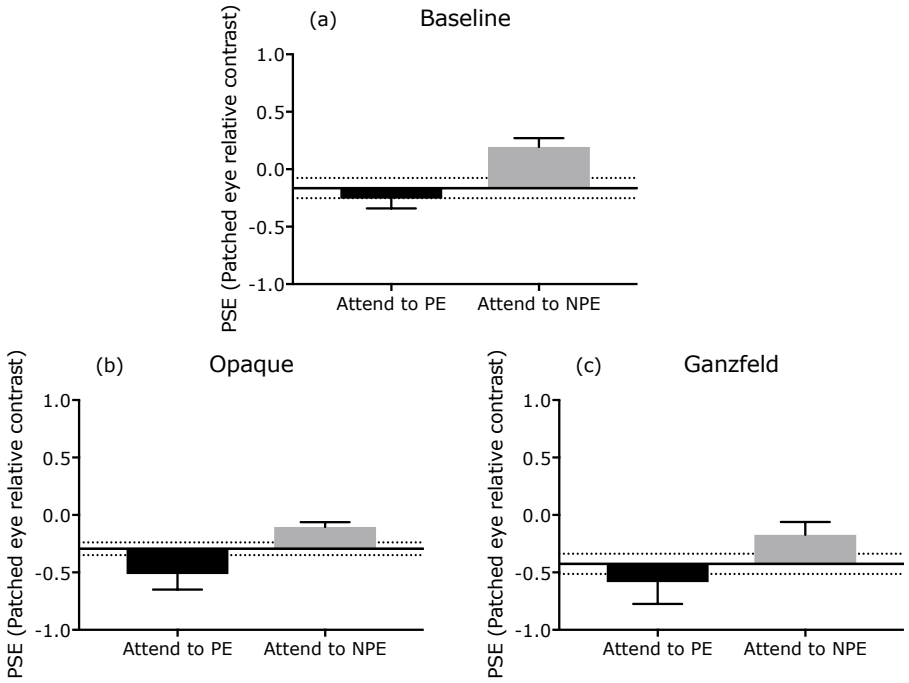


Figure 7.3: The mean PSE in terms of the patched eye relative contrast across the five subjects in Experiment 8a. The horizontal solid line marks the PSE measured in the neutral condition (the dotted lines indicate ± 1 SEM). The bars depict the PSE for attending to the patched eye (PE) and attending to the non-patched eye (NPE) conditions, plotted relative to the PSE for the neutral condition. The error bars are ± 1 SEM. The data are for (a) the baseline condition, or following 30 minutes of monocular patching with (b) an opaque patch or (c) a Ganzfeld lens.

an eye was examined for both eyes for a subset of participants in the current control experiment.

7.3.1 Methods

Three observers took part in this experiment (age range: 24–26 years, one female), including S31 who also completed Experiment 8a. The methods for this experiment were identical to those for Experiment 8a, except for the following aspects. The effect of monocular deprivation was only examined for the Ganzfeld patching, and this was conducted for both patching the left eye and patching the right eye (in separate sessions).

7.3.2 Results

Figure 7.4 shows the psychometric functions for an example observer (S33), plotted in the same manner as in Figure 7.2 (see figure legend). Similar to the results of Experiment 8a, selectively attending to the colour of an eye's stimulus shifted the psychometric functions in favour of the attended eye, measured in the baseline (i.e. without monocular deprivation), patching the left eye, or patching the right eye conditions. Moreover, regardless of the attentional state, patching the left eye produced shifts of the psychometric functions in the opposite direction to those following patching the right eye, and in both cases it was the previously patched eye that needed less contrast relative to the other eye's grating to dominate perception. For instance, although for this observer there is an intrinsic bias towards the right eye (indicated by a PSE less than zero), as shown in the neutral baseline condition (the solid curve in Figure 7.4a), patching the left eye eliminated the bias by enhancing the contribution of the left eye (the solid

curve in Figure 7.4b). This was in contrast to the increase of that right eye bias after the right eye was patched for 30 minutes (the solid curve in Figure 7.4c).

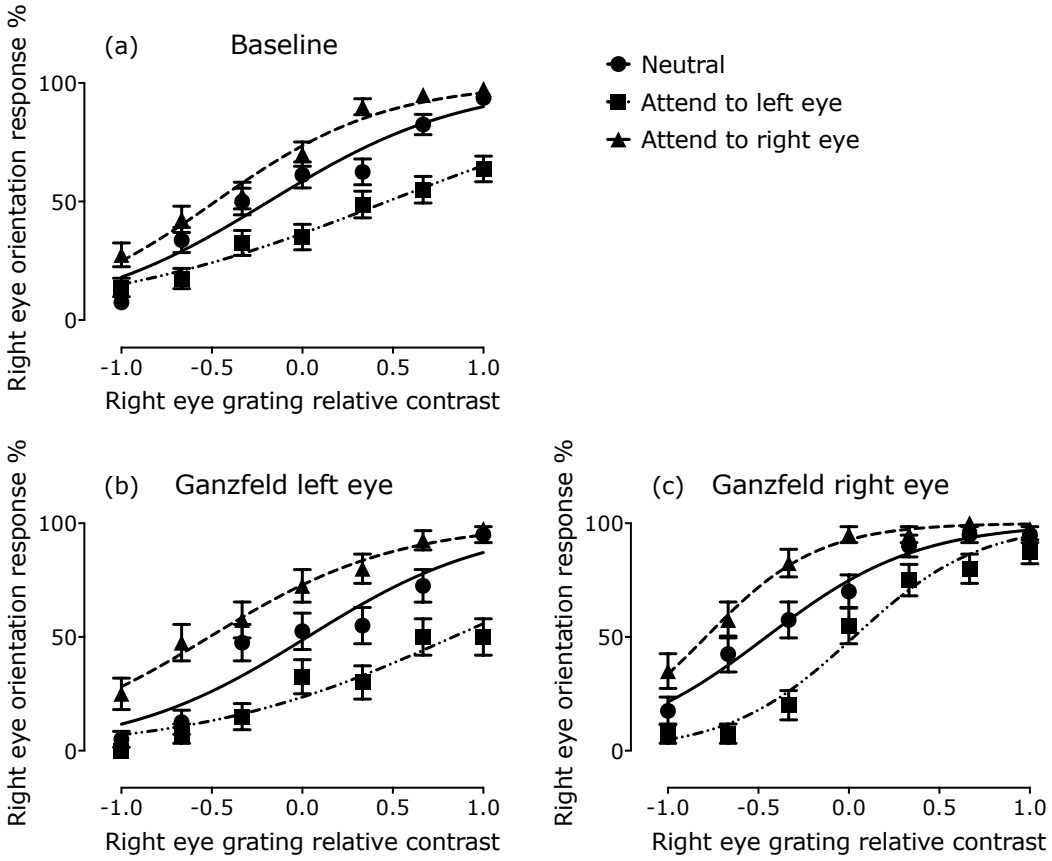


Figure 7.4: Psychometric functions of perceptual eye dominance measured in the neutral, attending to the left eye, or attending to the right eye condition, for participant S33 in Experiment 8b. The graphs are plotted in the same manner as in Figure 7.2, except that the abscissae represent the relative contrast of the right eye grating and the ordinates are the responses reporting right eye dominance. These data were obtained (a) in the absence of monocular patching (baseline), or following patching (b) the left eye or (c) the right eye using a Ganzfeld lens for 30 minutes.

The mean PSE (in terms of the right eye grating's relative contrast) for each condition is shown in Figure 7.5. Commensurate with the findings of Experiment 8a, the two types of attentional instructions had opposite effects on the PSE compared to that measured in the neutral condition (i.e.

when no instructions were provided to bias top-down attention selectively towards either eye's stimulus). These results confirm that explicit attentional instructions can modulate eye dominance during BR, by increasing the relative dominance of the attended eye. On top of the effect of attentional instructions[9], patching the left eye (Figure 7.5b) or the right eye (Figure 7.5c) increased or decreased the mean PSE relative to that measured without monocular patching (Figure 7.5a), respectively. Therefore these results clearly strengthen the conclusion drawn from Experiment 8a that eye dominance during BR can be independently modulated by selective attention and monocular deprivation.

7.4 General discussion

It is known that perceptual dominance during onset binocular rivalry is influenced by inter-ocular contrast differences, whereby the eye presented with the higher contrast dominates perceptual experience (see Figure 1.14; Song & Yao, 2009). The results of the two experiments in the current chapter support this phenomenon but also demonstrate the modulation of eye dominance by attentional instructions and monocular deprivation. These findings are consistent with previous observations that changes in perceptual eye dominance, produced by either attentional eye selection or short-term monocular deprivation, could be counteracted by introducing an inter-ocular difference in physical contrast (Chong & Blake, 2006; Spiegel et al., 2017). Furthermore, the current results also suggest that the effects of concurrent

[9]Although the magnitude of attentional modulation appeared to be larger when the left eye was patched than when the right eye was patched (compare Figures 7.5b and c), this was possibly due to the large variability in the results found in the neutral condition when the right eye was patched, rather than a genuine interaction between attentional modulation and monocular patching.

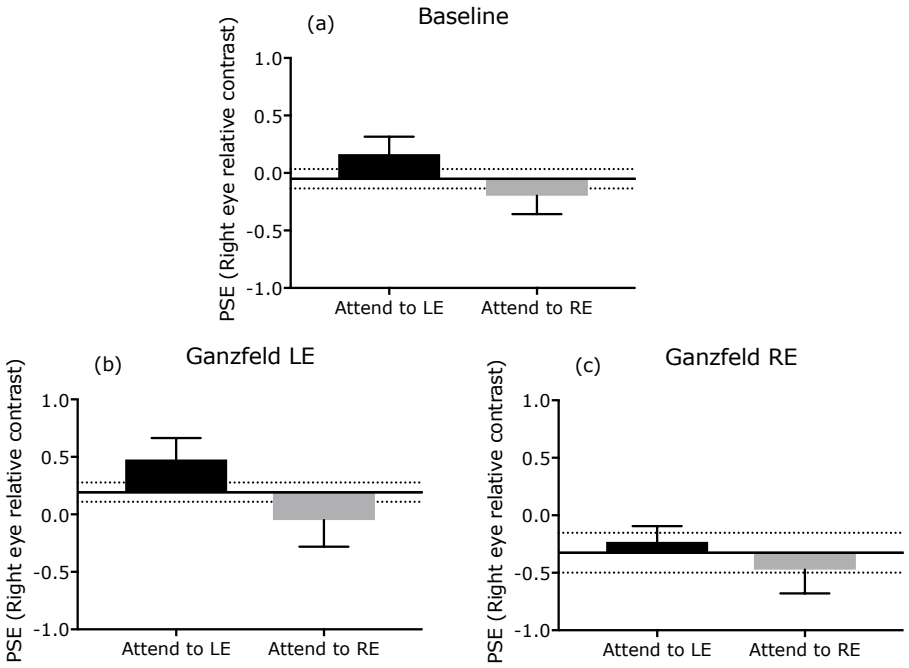


Figure 7.5: The mean PSE in terms of the right eye relative contrast calculated across the three subjects in Experiment 8b. The graphs are plotted in the same manner as in Figure 7.3, except that the two conditions with attentional instructions refer to attending to the left eye (LE) and attending to the right eye (RE). These data are for (a) the baseline condition, or following patching (b) the left eye or (c) the right eye using a Ganzfeld lens for 30 minutes.

attention and monocular deprivation seem to operate independently of each other. In addition, the changes to the psychometric function produced by both manipulations were a lateral shift but the shape (e.g. slope) of the function remained generally unaltered (see Figures 7.2 and 7.4). This implies that the dependence of eye dominance on the inter-ocular contrast difference was not changed by either attentional instructions or monocular deprivation.

It is possible to interpret the current findings within the framework offered by a simple model of inter-ocular imbalance as illustrated in Figure 7.6. This model highlights three sources of imbalance between the two eyes' visual processing. The first is in terms of the strength of sensory input when the eye dominance is measured (C_L and C_R). Second, the selective deployment of top-down attention to one eye's stimulus but not the other during the measurement also contributes to a perceptual bias towards the former (A_L or A_R). It can be noted that these two aspects of inter-ocular imbalance are both with respect to an instantaneous influence on perceptual dominance at the point in time when it is measured. The third aspect, by contrast, lies in the inter-ocular imbalance in the input strength during monocular deprivation, which takes place prior to the measurement of eye dominance. Interestingly, it seems that whether it has a concurrent (green and blue solid arrowed lines) or a subsequent effect (black dashed arrowed lines) determines the direction of the bias, indicating distinct natures for the two types of modulation. The effect produced by short-term monocular deprivation, possibly relying on a homeostatic mechanism that serves to maintain balanced inter-ocular interactions, shifts the relative dominance towards the previously less active eye. On the other hand, the imbalance between the visual encoding occurring within the two monocular channels

before any inter-ocular interactions (ϵ_L and ϵ_R, determined by low-level input, C_L and C_R, and higher-level attentional control, A_L or A_R) induces biased perception favouring the one with the stronger processing.

The present results suggested that none of the three factors specified above interacted with one another in modulating eye dominance. Specifically, the modulation of eye dominance by input strength and attentional instructions did not depend on each other. This is because the shape of the psychometric function was not influenced by providing attentional instructions. Similarly, the effect of monocular deprivation did not affect the modulation by input strength, also indicated by the unaltered shape of the psychometric function following monocular deprivation. Moreover, the results also demonstrated a non-significant interaction between the effects of attentional eye selection and monocular deprivation. In other words, the magnitude (or direction) of the shifts in eye dominance produced by providing attentional instructions was not altered following deprivation. Meanwhile, this finding also ruled out the possibility that monocular deprivation increases the relative dominance of the deprived eye by increasing the ability to selectively attend to that eye.

It is plausible that concurrent attentional eye selection and short-term monocular deprivation both have impacts on a common process—inter-ocular suppression (the lines ending in a red dot) that ultimately determines perceptual eye dominance. However, the modulation of the strength of inter-ocular suppression may be achieved differently for these two manipulations. Monocular deprivation may reduce the susceptibility of the deprived eye to inter-ocular suppression (I_{RL} or I_{LR}). This speculation is based on the findings of Experiment 5 (see Chapter 5) indicating that the shifts in eye dominance produced by monocular deprivation were driven

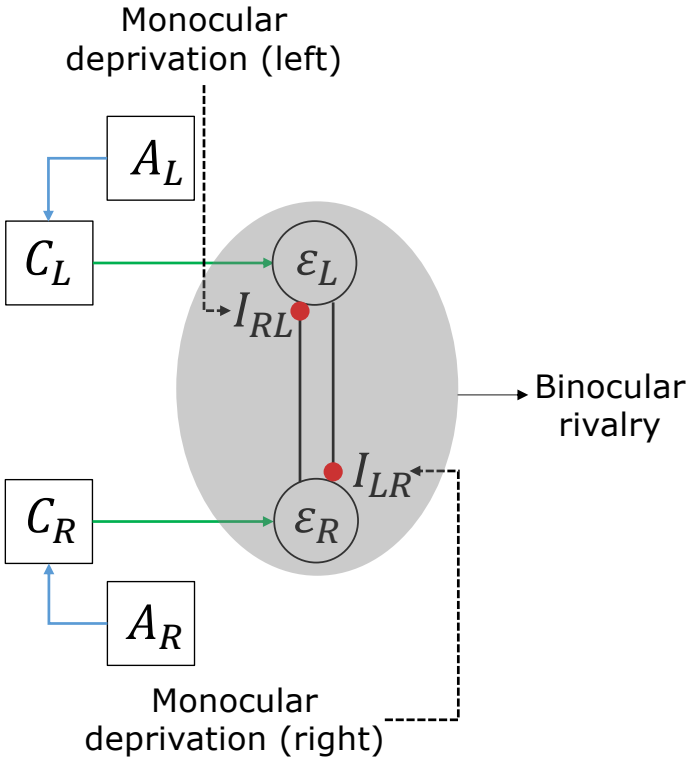


Figure 7.6: A plausible conceptual mechanism for interpreting the three types of factors that influenced eye dominance measured with binocular rivalry in Experiments 8a and 8b. The subscripts L and R represent the parameters for the left eye and the right eye, respectively. C_L and C_R are the strength of sensory input to the two eyes. These two parameters modulate the "gain pool" of each monocular channel (ϵ_L and ϵ_R; the modulation is indicated by the green arrowed lines) that determines the strength of inter-ocular suppression (black lines ending in a red dot). The "gain pool" is also modulated by selective top-down attention to either eye's stimulus, A_L or A_R, possibly through increasing the effective input strength of the attended eye (the blue arrowed lines indicate the modulation). Note that only one of the two stimuli can be selectively attended to at any one instant. Moreover, monocular deprivation of either eye may decrease the subsequent susceptibility of the previously deprived eye to suppression by the other eye (I_{RL} or I_{LR} shown as the red dots; the modulation is indicated by the black dashed arrowed lines), which alongside the "gain pool" also influences the strength of inter-ocular suppression[a]. Finally, the perceptual eye dominance during binocular rivalry is determined by the strength of inter-ocular suppression. See text for more details.

[a]Therefore, the strength of inter-ocular suppression is determined by both the two "gain pools" and the susceptibility of each eye to inter-ocular suppression.

by a reduction in the inter-ocular suppression of the deprived eye rather than monocular sensitivity of either eye. On the other hand, it is less likely for selective attention to directly affect inter-ocular inhibition, but rather it may target the monocular channel of each eye before any inter-ocular interactions. Carrasco et al. (2004) have demonstrated that selective spatial attention increases the apparent contrast of a stimulus presented to the attended location by increasing the contrast gain (see Figure 1.34). In addition, Dieter and Tadin (2011) proposed that attention plays a general role in resolving competition between conflicting visual information, regardless of whether it is between spatial locations or eyes (see Chapter 1, Section 1.12 for a discussion). Therefore, it is plausible that selective attention may act to increase the contrast gain of the attended eye (i.e. to increase the effective input strength, C_L or C_R).

The eye dominance plasticity shown by Dieter et al. (2016) indicated an interaction between attentional training and attentional eye selection. This observation contrasts with the current findings, implying that the plasticity induced by short-term monocular deprivation is distinct from that involved in perceptual learning. Indeed, it is believed that perceptual learning serves to increase sensitivity (e.g. Seitz & Watanabe, 2005). The current results however indicated no overall change in the sensitivity to stimulus signals (i.e. inter-ocular contrast difference) but a lateral shift in eye balance.

To summarise, the current experiments identified two independent mechanisms for modulation of perceptual eye dominance during BR: prior short-term monocular deprivation and concurrent attentional eye selection. Specifically, selectively attending to one eye's stimulus or patching one eye, reduced the contrast needed for the stimulus presented to that eye to dominate perception. Whether the deprivation was achieved using an opaque patch

or a Ganzfeld lens did not make a significant difference in the results, implying that the visual system may be more sensitive to inter-ocular imbalances in contrast information than in absolute luminance level. Importantly, the finding that eye dominance can be modulated by top-down attention, might have an important bearing on potential therapies for clinical anomalies of vision in that manipulating the attentional state of an observer may be useful in changing the sensory imbalance between eyes in adult amblyopia. This may serve as an alternative to the current patching therapies, which are thought to be effective only in young children and may have a range of adverse consequences on patients (Rutstein, 2005).

Chapter 8

General Discussion

8.1 Summary of findings

In this thesis, fundamental aspects of human binocular vision, such as inter-ocular suppression (in the context of conflicting inputs to the two eyes) and sensory eye dominance, have been investigated via a series of psychophysical experiments. The findings of these experiments have contributed new knowledge to the understanding of inhibitory inter-ocular interactions, placing important constraints on the mechanisms of binocular vision.

Setting out to explore the largely overlooked individual differences in inter-ocular suppression in individuals with normal binocular vision, Chapter 3 investigated whether these variations were predictable between two representative forms of inter-ocular suppression—binocular rivalry and continuous flash suppression. In addition to replicating the finding of a substantial difference between BR and CFS in their potency to evoke suppression (Tsuchiya et al., 2006), the results revealed moderate to strong positive correlations between the depth of suppression elicited by these two paradigms, which could not be accounted for by individuals' monocular contrast in-

crement thresholds. This finding indicates an overlap at certain stage(s) of the processing underpinning both BR and CFS, which may be related to the mechanisms encoding the differences between the two eyes' inputs (Katyal et al., 2016; Katyal et al., 2018; May & Zhaoping, 2016; May et al., 2012; Said & Heeger, 2013; H. R. Wilson, 2017), a signature of the inducing stimuli in both cases. In keeping with this result, correlations between BR dynamics and depth of suppression under dichoptic masking between orthogonal gratings have been previously reported (D. H. Baker & Graf, 2009b), supporting the notion of a common neural circuity responsible for the processing of inter-ocular conflict. The idea of binocular differencing channels was initially proposed, along with binocular summation channels, to support efficient stereo coding (Kingdom, 2012; Z. Li & Atick, 1994). Its basis was neurons that compute the sum of, or difference between, the inputs from the two eyes, and which has received some psychophysical support in that the binocular summation and differencing mechanisms appear to be independently susceptible to adaptation (May & Zhaoping, 2016; May et al., 2012). This idea may be useful in explaining distinct percepts under conditions of fusible and non-fusible stimuli, in the context of a general framework for understanding binocular interactions to be detailed in Section 8.2 below.

Another key aspect of the current thesis concerns the variations in susceptibility to inter-ocular suppression between eyes. Whilst asymmetric suppression between the two eyes is evidently present in amblyopia (Barrett et al., 2004; Ding et al., 2013a; Huang et al., 2012; Shooner et al., 2017; Zhou et al., 2018), previous studies have shown marked sensory eye dominance in BR even in the normal binocular visual system (e.g. Dieter et al., 2017a). The results of Chapter 3 also demonstrated differences between eyes

in terms of the thresholds measured under inter-ocular suppression evoked by BR and CFS, although a group-level analysis of the thresholds for the individuals' two eyes revealed that they were still significantly correlated in each case. Curiously, the patterns of signed eye dominance with respect to the depth of suppression evoked by these two paradigms appeared to be independent from each other. The implication of this finding is that the cause of the observed eye asymmetry is (at least in part) different under BR and CFS, despite the possible overlap in the mechanism computing the differences between eyes. In other words, after the inter-ocular difference is determined by the putative binocular differencing neurons, the assignment of weights to specify the contribution from each eye may be dissociable between BR and CFS. As the stimuli used to induce BR and CFS in these experiments only differed in terms of whether the suppressing noise pattern was static or dynamic, the source of this distinction in the patterns of eye dominance across people is likely to arise from discrepant temporal response functions between eyes in some individuals. If the eyes respond differently to temporally transient energy in the input to elicit inter-ocular suppression, the eye asymmetry would be revealed under conditions of CFS and scale with the amplitude of the transients (e.g. flicker rate), whilst it would be "silent" under conditions of BR where the stimuli in both eyes remain static. This is indeed the pattern of results found for some participants in Experiment 2, although further investigation is needed to address the reliability of this finding.

Chapter 4 sought to evaluate the possibility that the inter-individual and -eye variations under CFS result from latency differences between the two eyes. This hypothesis proposes that the marked variations in depth of suppression do not arise from differences in the intrinsic susceptibility to

inter-ocular suppression, but rather from differences in the propagation of information along the visual pathways for each eye, so that they do not converge simultaneously at a binocular site. If this is indeed the case, then individuals exhibiting weak suppression may still have the potential to elicit substantial suppression when an appropriate timing difference (i.e. SOA) is introduced between the presentations of suppressing and target stimuli. However, the result that the amplitude of suppression as a function of SOA, rather than the optimal SOA to trigger suppression, varied between individuals (and in some cases eyes) ruled out this latency difference hypothesis. An unexpected but intriguing finding is the negative SOA at which the greatest suppression was elicited, observed universally in the group of participants tested. That is, the noise onset had to precede the probe onset approximately 50–100 ms to achieve the maximum suppression depth. The cause of this result remains elusive, but it might reveal a latency for the temporally transient inputs to elicit inter-ocular suppression, offering a fruitful direction for future research. This result contrasts with the previous finding of another group that for peak suppression in CFS, the probe needed to be presented approximately 100 ms before the suppressing stimulus, at least when the data were pooled across individuals and between eyes (see Figure 4.2; Tsuchiya et al., 2006). This discrepancy is puzzling but highlights the importance of addressing individual differences and eye asymmetries in studies of inter-ocular suppression.

Chapter 5 aimed to extend the recent findings of eye dominance plasticity in the adult human visual system (Lunghi et al., 2011; Lunghi et al., 2013). After an eye was deprived of visual input for 2.5 hours, its contribution to binocular perception under conditions of BR and CFS was strengthened relative to that of the other eye. The results replicated Lunghi

and colleagues' original findings of the changes measured with BR dynamics—the stimulus presented to the previously patched eye was perceived for longer durations after the patch was removed. Moreover, using a CFS task, where each eye's contribution to inhibitory binocular interactions can be measured objectively as the threshold needed to detect a contrast increment in that eye, this experiment also located the shifts in eye dominance to a specific weakening of the susceptibility of the patched eye to inter-ocular suppression. This finding resonates with previous reports of a decline in the resting GABA concentration in V1 (Lunghi, Emir, et al., 2015) and an increased probability of mixed perception (Sheynin et al., 2019) following short-term monocular deprivation, which all support the conclusion of a patching-induced reduction in the level of inhibition.

To further elucidate the mechanisms that drive the shifts of eye dominance following short-term monocular deprivation, Chapter 6 compared the consequences on BR dynamics when different forms of distortion were applied to the visual input in one eye. The novel finding of these experiments was an enhancement of the contribution from the previously treated eye even when the input in this eye matched that in the other eye in terms of low-level attributes (e.g. luminance, contrast, shape information) other than an inversion of the image. That is, using a prism that inverted the image in one eye, binocular fusion was disrupted but the resultant image was unchanged in terms of the low-level energy. Crucially, the magnitude and time course of the shifts in eye dominance following this monocular treatment were comparable to those produced by monocular deprivation. The specific direction of the subsequent changes in the relative contributions of the two eyes postulates a role of inter-ocular imbalance during the treatment. A possible driver in the prism condition was the imbalance be-

tween eyes with respect to the allocation of top-down attention, whereby the more behaviourally relevant image (i.e. the upright image viewed by the non-treated eye) was selectively attended to for most of the time during the monocular inversion period. If this explanation holds, it implies equivalent influences of different sources of inter-ocular imbalance. That is, there is possibly a general factor capturing the level of imbalance between the two eyes' processing, regardless of the stages such imbalance arises, which then modulates subsequent sensory eye dominance. It thus provides useful insights into the stages of visual processing at which the underlying changes take place. Given the strikingly similar results observed in the three conditions, it seems plausible that these changes are determined at a later rather than early stage, where both low- and higher-level processes can elicit influences.

Finally, the findings of Chapter 7 demonstrated the separate influences on eye dominance (measured at onset of BR) produced by prior short-term monocular deprivation and concurrent selective attention. Selectively attending to an eye's stimulus during BR reduced the contrast required for it to dominate perception over the other eye, akin to the effects produced by monocular deprivation. The modulation of eye dominance by these two factors did not interact with each other, meaning that monocular deprivation does not affect how concurrent selective attention biases eye dominance during BR. This finding is important in specifying this concurrent attentional modulation of sensory eye dominance, which is in distinct nature from the possible sequential influences of attention on eye dominance (suggested by the findings of Chapter 6). That is, attentional eye selection during binocular processes instantaneously strengthens the relative contribution of the attended eye, whereas it may shift subsequent eye dominance in favour of

the previously less attended, "disadvantaged" eye, two effects that pull in opposite directions.

8.2 A synthesised framework

The findings of this thesis offer a basis to construct a general framework for understanding binocular interactions. As illustrated in Figure 8.1, a binocular percept is determined by the strength (e.g. contrast, luminance) of the inputs from both eyes (C_L and C_R for the left and the right eye, respectively) which independently contribute to a "gain pool" (ϵ_L or ϵ_R) for the corresponding eye's channel[1]. Whilst it is generally assumed equal weights (i.e. unity) for the two eyes' encoding processes under normal conditions, a gain efficiency parameter (μ_L or μ_R) is proposed here to allow for asymmetric processing. Notably, W. J. M. Levelt (1966a) expressed "the law of complementary shares" to describe situations where the contributions from the two eyes are reciprocally constrained. It is worth pointing out that the gain efficiency proposed in Figure 8.1 is a distinct process that independently weights the monocular processing in each eye, but it does not describe the relative contributions from the two eyes which may be determined at a later stage, where inter-ocular interactions take place.

8.2.1 Two separate pathways for fusible and non-fusible conditions

The experiments conducted here have focused on inhibitory inter-ocular interactions, and the existence of a binocular differencing channel is sug-

[1]Note that the "gain pool" denoted here refers to the output of each monocular channel before any inter-ocular interactions occur.

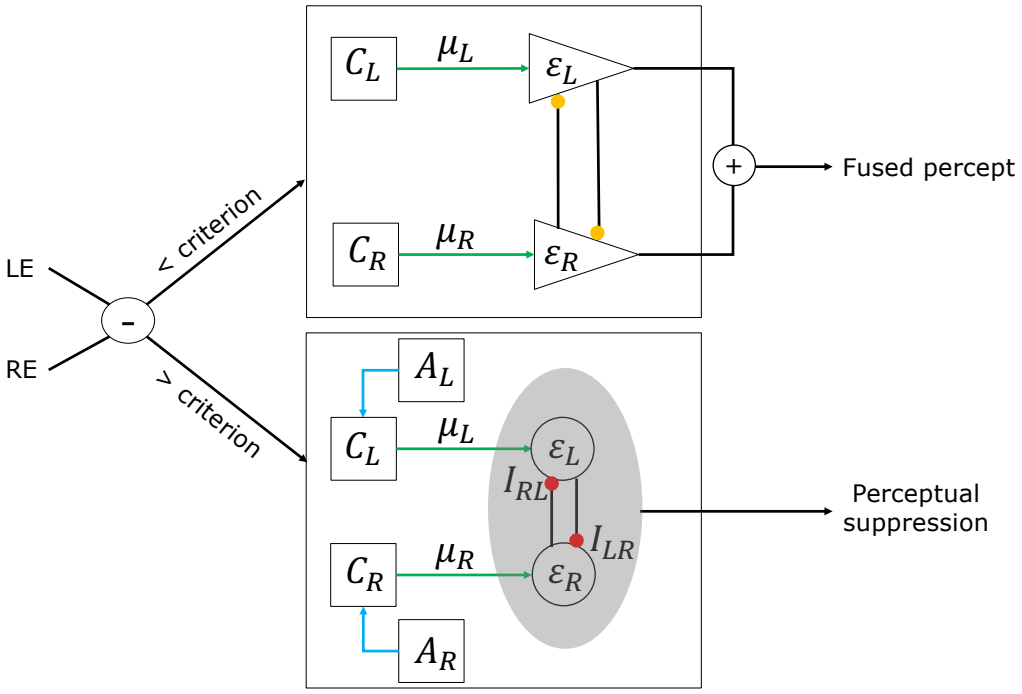


Figure 8.1: A general framework for understanding binocular interactions. A binocular differencing channel first computes the difference in contour between the stimuli presented to the left eye (LE) and the right eye (RE). When the inter-ocular conflict is sufficiently weak, the two eyes' signals go through the fusible pathway (top), otherwise they undergo the non-fusible pathway (bottom). C_L and C_R are the strength of the inputs to the two eyes. The input from each eye then contributes to a "gain pool" (ϵ_L or ϵ_R), weighted by a gain efficiency shown by the green arrowed lines (μ_L or μ_R). The differences between the fusible and non-fusible pathways are with respect to the nature of inter-ocular interactions. In the fusible pathway, the gain of each monocular channel undergoes gain control by the other eye through divisive inhibition, depicted by the lines ending with a yellow dot. Thus such inhibition is dependent on the monocular gain before inter-ocular interactions. The output of such a process is ultimately combined between the two eyes to form a fused percept. In the non-fusible pathway, the input strength of each eye is subject to modulation by top-down attentional eye selection (A_L or A_R) by increasing the contrast gain of the attended eye. The monocular gain of each eye undergoes another type of inter-ocular inhibition, possibly elicited by opponency units proposed by Said and Heeger (2013) that are activated by preferred features in one eye but inhibited by the same features in the other eye. The strength of such inter-ocular inhibition is represented by the lines ending with a red dot, which is dependent on both the monocular gain of each eye and the inhibition level produced by the opponency units (I_{RL} or I_{LR}, red dots). Consequently, the output of these processes (the shaded area) leads to perceptual suppression of one or the other image. See text for more details.

gested both by the present results (see Chapter 3 and Chapter 5), and by physiological evidence elsewhere (Katyal et al., 2016; Katyal et al., 2018). In those studies, stimuli presented to the two eyes were tagged with different frequencies (Figure 8.2). The EEG responses recorded in early visual cortex were found to increase alongside the conflict between the two eyes' patterns, even when the stimulus contrast was decreased. This effect was dampened by prior adaptation to inter-ocular conflict, which coincided with a lowered likelihood of perceptual suppression (Katyal et al., 2016; Katyal et al., 2018). Other work also suggests that inter-ocular suppression arises from a mismatch in contours between the two eyes' stimuli and increases as the inter-ocular differences are increased (e.g. Varela & Singer, 1987). It is therefore plausible to suggest that the computation of inter-ocular differences occurs at an early stage and the decoded conflict in contour determines the nature of subsequent binocular interactions—whether fusion or suppression[2] takes places. A feature of the proposed framework is that these two perceptual consequences are mutually exclusive (Blake & Boothroyd, 1985; Blake, Yang, & Wilson, 1991; Georgeson & Wallis, 2014; Harrad, McKee, Blake, & Yang, 1994; O'Shea, 1987) and depend on binocular disparity (Buckthought, Kim, & Wilson, 2008; H. R. Wilson, 1977, 2017). In compatible with this idea, H. R. Wilson's (2017) model of binocular vision also suggests that there are distinct classes of interneurons that are responsible for inter-ocular inhibition in fusible and rivalrous conditions. Differentiating between the two conditions is necessary to explain the lack of rivalry between orthogonal orientations when a binocular plaid stimulus is used

[2]To reiterate, although the term inter-ocular suppression is sometimes also used to describe the deterioration in sensitivity to detect a stimulus in one eye by an identical stimulus (i.e. mask) presented to the corresponding location in the other eye (e.g. Meese et al., 2006), in the present work it refers specifically to the perceptual suppression in the presence of inter-ocular conflict where binocular fusion cannot be attained.

(also see Said & Heeger, 2013). Indeed, there is psychophysical evidence showing uncorrelated dichoptic masking effects, measured as elevation in thresholds, when the two eyes' stimuli were fusible and when they were non-fusible due to a sufficient difference in orientation (Baldwin & Hess, 2018)[3]. This supports independence between fusion and suppression. A physiological study in cat has also revealed a small range of inter-ocular differences in orientation within which binocular facilitation in the response of striate neurons occurred (Sengpiel & Vorobyov, 2005), commensurate with Panum's fusional range. When the stimulus orientation in the contralateral eye became more discrepant from that viewed by the ipsilateral eye, a reduction in response was observed instead, marking the presence of inter-ocular inhibition (also see Varela & Singer, 1987). Moreover, this response reduction was absent with the administration of a GABA antagonist whilst binocular facilitation was unaffected, implying a role of GABAergic inhibition in the mediation of inter-ocular suppression. In the context of the present findings, this is likely to be the physiological basis for both BR and CFS, resulting in a correlation between the depth of suppression measured in each case.

Fusion occurs when the inter-ocular conflict in contour detected by the hypothetical binocular differencing channel is sufficiently small. There are a number of models proposed to account for the binocular processes evoked by fusible stimuli, that capture some features of the data measured behaviourally and/or physiologically (D. H. Baker & Wade, 2017; Ding et al., 2013a, 2013b; Ding & Sperling, 2006; Meese et al., 2006; Moradi & Heeger, 2009). Of relevance here are the inhibitory interactions described in

[3]However, it cannot rule out the possibility that the lack of correlation between the two types of dichoptic masking reported was due to the additional elevation of threshold by binocular fusion in the parallel condition compared to the cross-orientation condition.

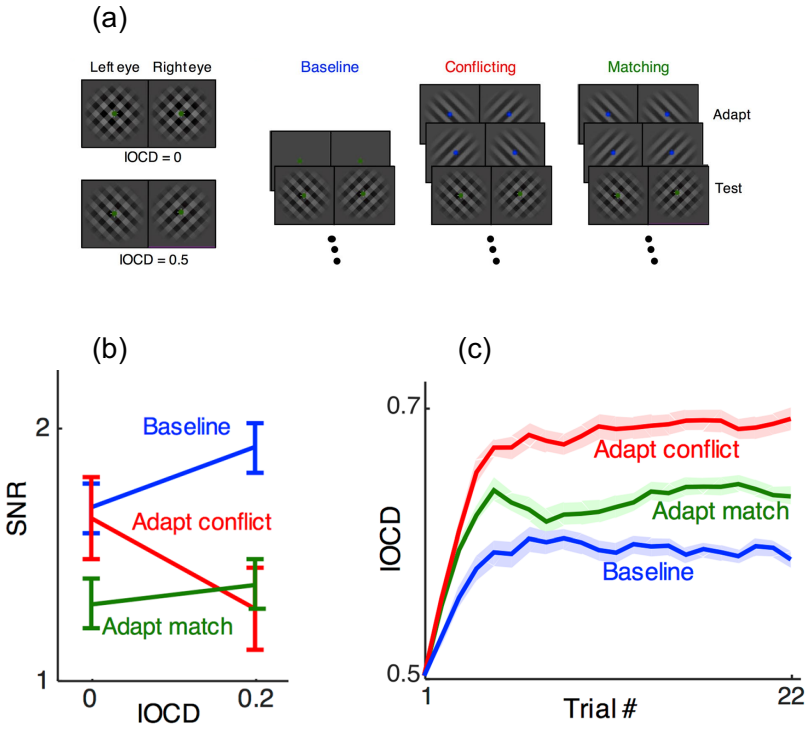


Figure 8.2: Evidence of neurons sensitive to inter-ocular conflict. (a) The two eyes were stimulated with plaid stimuli, each tagged with a distinct frequency while SSVEP responses were recorded in early visual cortex. When the two eyes' stimuli were identical the inter-ocular contrast difference (IOCD) was 0 but it was varied by decreasing the contrast of one of the two plaid components in each eye (different components for the two eyes). Before the measurement was taken, the participant was exposed to stimuli incompatible (conflicting) or identical (matching) between the two eyes, in order to adapt neurons that detect inter-ocular conflict or those encoding matching features, respectively. Performance in the absence of prior adaptation was also tested (baseline). (b) The signal-to-noise ratio (SNR) of the intermodulation frequency (difference between the two eyes' frequencies) as a function of IOCD. With no adaptation, the response increased with IOCD, even when the total contrast of the stimuli decreased. This effect was diminished after adapting to inter-ocular conflict but was unaffected by adaptation to matching features between the two eyes. (c) The suppression threshold in terms of IOCD at which the participant reported suppression in half of the trials. Suppression here is defined as perceiving unequal contrasts for the two components of the plaid, because when the two eyes' plaid patterns were fused the two components were supposed to be the same in contrast. Adapting to inter-ocular conflict increased the subsequent suppression threshold to a greater extent than did adapting to matching features. Adapted from Katyal et al. (2018).

these models that are characterised by the process of contrast gain control. This idea attributes the observed nonlinearities in the response functions of binocular summation to divisive inhibition. Specifically, it is thought that the response to the input from one eye is normalised by the input from the other eye (i.e. inter-ocular gain control) or both eyes (i.e. binocular gain control[4]). The strength of inter-ocular gain control is represented in Figure 8.1 by the lines ending with a yellow dot, and is dependent on the monocular gain of each eye's channel before any inter-ocular interactions (ϵ_L or ϵ_R). It is assumed that the output of the gain control process is ultimately combined between the two eyes, giving rise to a fused percept.

When it comes to the conditions in which fusion cannot be attained due to incompatible stimuli presented to the two eyes, perceptual suppression is presumed to arise. As the two eyes' stimuli are dissimilar, the observer can selectively attend to either eye's image. Thus a unique feature in this case, distinct from the conditions with binocularly fusible stimuli, is that the monocular gain of each eye's channel is subject to the influence of top-down attentional eye selection, represented by the blue arrowed lines in Figure 8.1. This idea is supported by evidence demonstrating an enhancement of contrast gain by selective attention (Cameron et al., 2002; Carrasco et al., 2004; Chong & Blake, 2006; Reynolds & Chelazzi, 2004; Reynolds & Pasternak, 2000) which has been discussed in detail in Chapter 1, Section 1.12.

Another property of this pathway that differs from the process leading to fusion lies in the nature of the inter-ocular interactions. Although neural inhibition presumably underlies both cases, the distinct perceptual consequences (fusion vs. suppression) suggest that there are important dif-

[4]This can be considered as the combination of self gain control, which can be implemented with the gain efficiency parameter μ, and inter-ocular gain control.

ferences. The inter-ocular inhibition relevant to suppression is represented by the lines ending with a red dot in Figure 8.1. Whilst the strength of such inhibition is also modulated by the monocular gain of each eye's channel (ϵ_L or ϵ_R) as in the case of fusion, an extra parameter (I_{RL} for the inhibition from the right eye to the left eye or I_{LR} for that in the converse direction) is proposed here that additionally weights the inhibition strength. The physiological substrate of such a parameter may be related to the activity of a binocular opponency channel, a notion similar to the concept of a binocular differencing channel but proposed specifically to explain binocular rivalry (see Figure 1.8; Said & Heeger, 2013). It is suggested that there is a set of opponency units that elicit inhibition from one eye to the other and another set for the converse direction. The inhibition produced by such units depends on the degree of conflict in contour between the two eyes' stimuli, weighted by the neuronal activity of the two monocular channels (so it is presumably dependent on the input strength). Alternatively, this parameter (I_{RL} or I_{LR}) may be interpreted conceptually as the intrinsic susceptibility of an eye to inter-ocular inhibition elicited by the other eye. In either case, the importance of such a parameter is that it allows for the adjustment of inter-ocular suppression of an eye (e.g. by short-term monocular deprivation, as will be discussed below) without affecting the monocular gain of each eye's channel, consistent with the results of Experiment 5. Finally, this process outputs perceptual suppression in the form of BR, CFS or other inter-ocular suppression phenomena (e.g. flash suppression), depending on the stimuli and paradigms employed. The identification of the underlying mechanisms is beyond the scope of the present general framework, but a likely candidate is mutual inhibition and self-adaptation (e.g. H. R. Wilson, 2007; for a discussion, see Chapter 1, Section 1.7).

8.2.2 In the context of short-term monocular distortion

The above framework is also useful for the interpretation of the findings regarding short-term monocular distortion. It is helpful to consider the binocular processes during monocular treatment and those during the post-treatment measurement separately. They both feed through the framework in the same manner, but the output from the processes underlying monocular treatment will alter the parameters of the processes during subsequent measurement.

An important constraint comes from previous work showing different consequences of monocular distortion on BR and binocular phase combination tasks (Bai et al., 2017; Zhou et al., 2014). That is, after several hours' monocular treatment where an eye's image was scrambled in phase but its Fourier amplitude spectrum matched that of the non-treated eye (which has received normal visual input), shifts towards the previously treated eye were only revealed when eye dominance was measured with a BR task but were absent if a binocular phase combination task was used. This phenomenon differs from the comparable results obtained using the same two tasks and an opaque patch or a translucent lens was used to produce monocular deprivation (see Chapter 6; also see Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). It is implied here that the inter-ocular interactions occurring in fusible and non-fusible conditions may be affected differently by monocular treatment, even though eye dominance was changed similarly in both cases. Consistent with this hypothesis, Baldwin and Hess (2018) have shown that the effect of monocular deprivation measured with fusible stimuli was not significantly correlated with that measured with non-fusible stimuli across

their group of observers (see Figure 1.28).

A critical feature of the effects of short-term monocular distortion is the specific direction of the changes in eye dominance. This implies that the mere disruption of fusion cannot be the sole cause of these effects as it does not specify which eye is to be boosted (cf. Bao et al., 2018; Klink et al., 2010). Instead, it is conceivable that imbalanced visual processing between the two eyes during the monocular treatment led to a relative enhancement of the previously "disadvantaged" eye. One possibility is that the visual system adapts to the imbalance and adjusts the reference balance point accordingly such that the weighting of each eye's contribution to binocular interactions is modified. That is, whenever both eyes are stimulated simultaneously, the visual input to the previously treated eye is regarded as stronger than it would be at the baseline level before treatment. This account is intuitive and makes it relatively straightforward to interpret the changes in relative contributions from each eye to binocular combination under fusible conditions. However, it fails to explain the present result that the inter-ocular suppression of the non-treated eye under CFS was unaffected. Under non-fusible conditions, alternatively, it could be that the visual system is compensating for the relatively inactive response of the previously treated eye (which may be in terms of input strength, top-down attentional allocation, or any other forms of modulation), to ultimately rebalance visual processing between the two eyes. This idea could account for the results of the prism condition in Experiments 6 and 7, in that although the input energy in the two eyes was balanced, an attention-driven imbalance in the processing of the two eyes' information has possibly engaged subsequent compensatory mechanisms. Lunghi, Emir, et al. (2015) have shown a reduced level of GABAergic inhibition in V1 following short-term

monocular deprivation, which was positively correlated with the shift towards the previously patched eye measured with BR across the same group of participants. This points to a change in the excitation-inhibition balance, which is thought to be crucial for homeostatic plasticity in sensory systems (Turrigiano, 2003). Therefore, it is tempting to speculate that the visual system rebalances processing between the two eyes (under non-fusible conditions) through decreasing inhibition of the eye that has been less active. In support of this suggestion, the results of Experiment 5 and those obtained from previous work suggest that the changes produced by monocular deprivation were in terms of inter-ocular inhibition, which cannot be sufficiently explained by monocular changes in either eye (if any) (Chadnova et al., 2017b; Lunghi et al., 2011; Sheynin et al., 2019).

To reconcile the findings regarding monocular phase-scrambling (Bai et al., 2017; Zhou et al., 2014), we speculate that the reference balance point is only subject to the influence of any imbalance directly arising from the difference in input energy between the two eyes (C_L and C_R). Such an imbalance was absent when the Fourier amplitudes of the two eyes' images were kept the same. On the other hand, it is possible that the phase-scrambled eye was suppressed through BR (due to the incompatibility of the images viewed by the two eyes) a greater proportion of time than the non-treated eye. Indeed, previous studies have shown that a phase-scrambled image is less dominant than a normal image viewed by the other eye under conditions of BR (Alais & Melcher, 2007) or CFS (Shui'er Han et al., 2018). In that case, the inter-ocular inhibition (I_{RL} or I_{LR}) from one eye to the other is higher than the reciprocal inhibition, giving rise to asymmetric processing between the eyes. Following this principle, it is expected that only binocular interactions under non-fusible, rather than fusible conditions,

are sensitive to periods of monocular phase-scrambling.

8.2.3 Summary

The proposed framework provides a general theory to reconcile the results of all experiments detailed in this thesis and those arising from previous work. It incorporates the notion of a binocular differencing channel that determines which of the two types of inter-ocular inhibitory interactions takes place—inter-ocular gain control between fusible stimuli and inter-ocular suppression ("winner-take-all") between incompatible stimuli. Moreover, the mechanisms of short-term monocular distortion that alter eye dominance in fusible and non-fusible stimuli are distinguished within such a framework, a feature absent from previous theories of binocular vision.

8.3 Future directions

8.3.1 Feature specificity of eye dominance

One of the results of Experiment 1 was the independent eye asymmetries in the depth of suppression elicited by BR and CFS. This implies some degree of dissociation between the two processes, even though the suppression was correlated between the two measures for each eye. Past research indicated some discrepancies in the feature selectivity between the depth of suppression under BR and CFS (Holopigian, 1989; Ledgeway et al., 2013). That is, whilst the suppression measured as a reduction in sensitivity under CFS was modulated by inter-ocular luminance and contrast differences (Ledgeway et al., 2013), that under BR was found to be independent of these stimulus properties (Holopigian, 1989). This raises the question of whether

eye dominance measured in each case is subject to the same degree of feature selectivity. Addressing this unresolved issue may be helpful in explaining the independent patterns of eye dominance found in these two inter-ocular suppression phenomena. Notably, it is common that the two eyes in amblyopia which typically involves extreme eye dominance have distinct spatial-frequency dependencies, suggested by both physiological (Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998) and behavioural observations (Ciuffreda, Levi, & Selenow, 1991). An implication here is that the eye asymmetry in amblyopia is feature dependent, which has been indeed shown by some recent studies (Beylerian et al., 2020; Kwon, Wiecek, Dakin, & Bex, 2015). Therefore, feature tuning properties may potentially serve as an important metric for distinguishing different natures of eye dominance.

8.3.2 Multiplicative noise as an account of eye asymmetries: inter-ocular suppression in normal and amblyopic vision

In Experiment 2 the asymmetric suppression found in some observers seemed to increase when the noise refresh rate was increased, implying the presence of multiplicative noise in the processing channel of the non-dominant eye. This is also believed to be one of the sources of eye asymmetries in amblyopia (D. H. Baker et al., 2008; Levi & Klein, 2003; Levi et al., 2007). These modelling studies suggested that including a component of signal-dependent noise in the amblyopic eye's channel, before any inter-ocular interactions, could reasonably explain the empirical data. It is possible that such noise exists in clinically typical individuals who show eye asymmetries, whilst it reaches a pathological level in amblyopia. Whether this is the case remains

to be seen, and has important implications for understanding whether the distinction between sensory eye dominance in the healthy visual system and that in amblyopia is quantitative or qualitative.

8.3.3 Latency of the flash under CFS

An unexpected finding of Experiment 4 was that the peak CFS occurred at a negative SOA (noise onset proceeding the probe onset) for all the participants tested. Therefore, a latency of approximately 50–100 ms is optimal for the flash stimulus to produce inter-ocular suppression of the probe. It is possible that this latency can be changed by manipulating stimulus attributes, as previous studies have revealed that contrast alters response latencies of visual neurons (e.g. Stevens, McGraw, Ledgeway, & Schluppeck, 2009). This offers an interesting avenue to be researched, which might shed light on the temporal characteristics of CFS that may be distinct from other types of perceptual suppression. For example, if the optimal temporal difference between the flash stimulus and the target is independent of stimulus properties other than flash rate, an account of a minimum number of flash required to trigger maximum suppression that is specific to CFS would be favoured. By contrast, it may simply reflect a stimulus-specific latency difference (irrespective of the form of inter-ocular suppression) if it can otherwise be modulated by stimulus properties.

8.3.4 Opponency channel

The idea of a binocular opponency channel seems to commensurate with the present findings, and it is worth testing its predictions within the context of short-term monocular treatment. The framework proposed in Section 8.2

suggests that it is the inhibition of the previously treated eye, elicited by the opponency units for the non-treated eye's channel[5], that can be altered by monocular treatment. A signature of this opponency channel is that mixed perception (i.e. non-exclusive percepts under BR) should increase following adaptation to inter-ocular conflict, reflecting diminished suppression elicited by such a channel, which has received empirical support (Klink et al., 2010; Said & Heeger, 2013). It would be informative to establish if such an effect is changed following monocular treatment. This would test the hypothesis that the altered activity of the opponency channel drives the shifts in eye dominance.

8.3.5 The role of top-down attentional eye selection in driving the shifts in eye dominance following short-term monocular treatment

The findings of Chapter 6 suggest that monocular deprivation of low-level sensory input is not a prerequisite for producing shifts in eye dominance. Indeed, the results of the prism condition suggest that the top-down attentional eye selection, during the monocular inversion period, can drive the subsequent enhancement of the contribution from the treated eye to binocular perception. Nevertheless, the activities the participants undertook during the treatment period were not constrained or monitored in the present experiments, such that attention was not strictly controlled. This could be directly tested in future experiments by manipulating the degree to which selective attention is required during the monocular treatment.

[5]The response of these units is activated by the preferred features in the non-treated eye but inhibited by those in the treated eye, which ultimately inhibits all the features in the treated eye (see Said & Heeger, 2013).

If top-down attention does play a role in the prism condition, one might expect to find larger effects when participants are required to perform a task whilst wearing the prism that requires them to actively attend to the eye receiving the normal visual input. This was indeed the pattern of results we found in a pilot study. During an hour of monocular inversion participants either did a jigsaw puzzle, which was attentionally demanding (active condition), or simply stared at a plain curtain (passive condition), before they were tested in a BR percept tracking task. A large shift in eye dominance towards the previously treated eye was observed in the active condition only, but the effect was small or absent in the passive condition (Figure 8.3). These results strongly support a critical role of attention in driving eye dominance plasticity, at least in the prism condition.

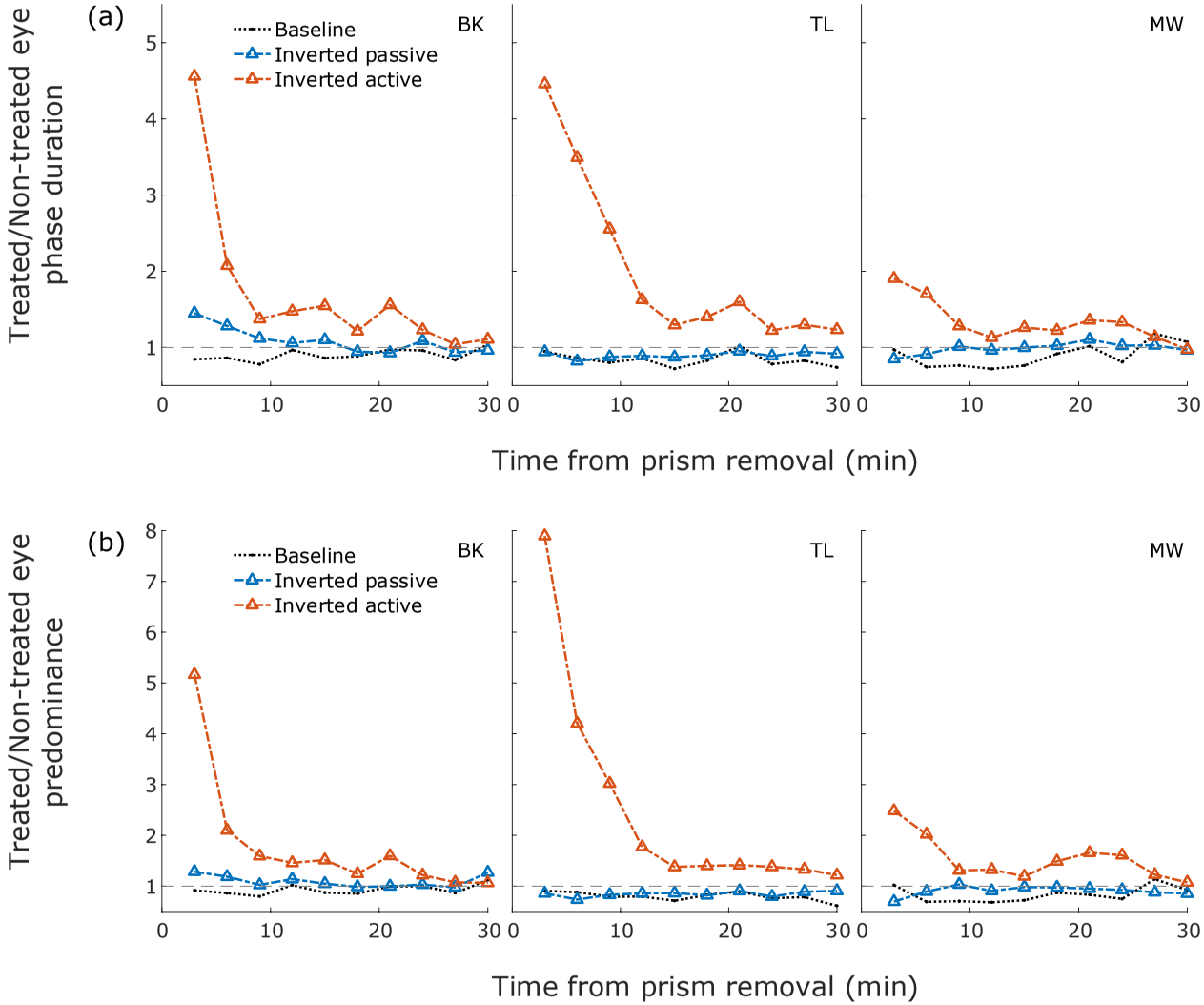

(a)
Baseline
Inverted passive
Inverted active
BK
TL
MW
Treated/Non-treated eye phase duration
Time from prism removal (min)
(b)
Baseline
Inverted passive
Inverted active
BK
TL
MW
Treated/Non-treated eye predominance
Time from prism removal (min)

Figure 8.3 *(previous page)*: The time course of the relative eye dominance following an hour of monocular inversion for each of three observers in a pilot study. Participants either did a jigsaw puzzle (active) or simply stared at a plain curtain during the monocular inversion period (passive). The results for the data measured without prior monocular inversion (baseline) are also shown. (a) The ratio of mean exclusive phase duration experienced by the treated eye to that for the non-treated eye as a function of the time elapsed since removing the prism. The dashed horizontal line signifies an independence of mean phase duration on whether the stimulus was presented to the previously treated or non-treated eye. (b) Same as (a) but in terms of stimulus predominance.

Interestingly, Chapter 7 has shown that the concurrent attentional modulation of eye dominance is unaffected by monocular deprivation of sensory input. However, whether it is subject to the effect of prior experience of monocular inversion where top-down attention seems to play a crucial role has yet to be investigated. The framework proposed in Section 8.2 (see Figure 8.1) assumes specificity of the alteration of inter-ocular inhibition of the previously treated eye in response to any form of imbalance in the two eyes' processing. This in turn predicts that the concurrent attentional modulation of eye dominance should not be influenced by prior experience of monocular inversion, like in the case of other forms of monocular treatment. Future research could investigate the validity of this prediction. If, unlike the opaque and Ganzfeld conditions, the effect of monocular inversion on eye dominance interacts with the instantaneous attentional effects, this would suggest distinct systems of eye dominance plasticity driven by low-level and higher-level processes, and thus corresponding modifications of the proposed framework would be required.

8.4 Conclusion

The series of experiments in this thesis have made an important contribution to the understanding of two crucial aspects of binocular vision—inter-ocular suppression and sensory eye dominance. On the basis of the current findings, a novel theoretical framework has been proposed, incorporating the notion of a binocular differencing channel, to explain inter-ocular interactions leading to binocular fusion and those resulting in perceptual suppression. The effects of short-term monocular treatment can also be readily interpreted within this framework, providing a unified approach to the study of eye dominance plasticity.

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Appendix A

Results of permutation tests in Experiment 5

Table A.1: The results of permutation tests (number of permutations: 10000), indicated by p values, comparing individuals' mean or median phase durations (exclusive noise or grating percept) between pre- and post-patching measurements in Experiment 5. These tests were performed for the patched and the non-patched eyes separately. The null hypothesis was that monocular patching had no influence on the mean or median duration.

Observer	Patched eye		Non-patched eye	
	Noise	Grating	Noise	Grating
		Mean		
S1	.016	.235	.067	$< .001$
S7	.091	.040	.011	.005
S8	$< .001$	.016	.914	.004
S21	.980	.854	$< .001$	.004
S4	.001	$< .001$	$< .001$	.020
S20	$< .001$	.189	$< .001$	$< .001$
		Median		
S1	.010	.129	.154	.005
S7	.033	.013	.002	.022
S8	$< .001$	.372	.025	.008
S21	.617	$< .001$	.918	.003
S4	.004	$< .001$	$< .001$	.049
S20	.003	$< .001$	.211	$< .001$