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PERCEPTUAL LEARNING OF BINOCULAR INTERACTIONS

By

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B.S. East China Normal University, 2005

A Dissertation

Submitted to the Faculty of the

Graduate School of University of Louisville

in Partial Fulfillment of the Requirements

for the Degree of

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Louisville, Kentucky

August, 2011

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A Dissertation Approved on

June 7, 2011

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Dissertation Director (Zijiang He)

Heywood M. Petry

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Martha Bickford

DEDICATION

This dissertation is dedicated to my parents

Mr. Shuijian Xu

and

Mrs. Qifeng Gui

who have given me invaluable love and support.

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I would like to thank my mentor Dr. Zijiang He, for his great guidance and patience. I would also like to thank the other committee members, Dr. Martha Bickford, Dr. Barbara Burns, Dr. John Pani, and Dr. Heywood M Petry, for their helpful comments and advice. Also, I want to give many thanks to my lab members Yong Su and Xuan Li, for their continuous assistance. I would also like to express my thanks to all the participants in my experiments, for their cherish time and effort. Finally I would like to thank Andrew Haun for his constant encouragement.

ABSTRACT

PERCEPTUAL LEARNING OF BINOCULAR INTERACTIONS

Jingping Xu

June 7, 2011

This dissertation focuses on the mechanisms and implications of perceptual learning of binocular interactions. Perceptual learning is an important means of adapting to the changing environment, demonstrating the possibility of neural plasticity in adults and providing a powerful approach to investigate dynamic processes in the mature perceptual system. Most studies on perceptual learning have focused on learning mechanisms that target excitatory circuits. However, we recognize that the inhibitory circuits also play a critical role in cortical plasticity, as shown by growing evidence from neurophysiological studies, and that the inhibitory connection is more dynamic than the excitatory connection in adult visual cortex. Thus, our goal is to design a psychophysical method that exploits the contribution of the inhibitory circuits to perceptual learning. This in turn helps us to implement more efficient learning paradigms for visual training.

Our study capitalizes on properties of the binocular visual system, a good system for exploring both excitatory and inhibitory mechanisms. We first measured local Sensory Eye Dominance (SED) and showed that excessive SED can impede stereopsis ability. To reduce SED, a typical perceptual training paradigm (Push-only protocol) would only

stimulate the weak eye to target the excitatory network. In contrast, we designed a novel Push-Pull training protocol to target both the excitatory and inhibitory networks. By presenting binocular rivalry stimuli to both eyes, the push-pull protocol can excite the visual pathway of the weak eye (push), while inhibiting the visual pathway of the strong eye (pull). We found that the push-pull training protocol, mainly affecting the early visual processes, is more effective than the push-only protocol in reducing SED and enhancing stereoacuity, even beyond the focus of top-down attention through a stimulus-driven mechanism. We further demonstrated that the perceptual learning induced by the push-pull protocol involves both feature-based and boundary-based processes, and that the learning effect can be generalized to other stimulus dimensions within early feature channels. Therefore, our psychophysical study demonstrates the important role of inhibitory synaptic circuits in neural plasticity of the adult brain, and that our push-pull training protocol can be a more effective clinical training paradigm to treat amblyopia.

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CHAPTER 1

BACKGROUND AND INTRODUCTION

1.1 Importance of perceptual learning

Researchers have been showing great interest in the study of perceptual learning because it not only demonstrates the clinical possibility of neural plasticity in adults, but also because it provides a dynamic implementation for modeling of a perceptual system. From early case reports and studies of brain injury and recovery, researchers began to realize that a certain level of neural plasticity still exists in adults even though they have long passed their “critical period” (Sousa, 2001). Such brain plasticity is usually expressed as structural and functional compensation from other brain regions for the injured region. Studies of blind individuals (Hotting, Rosler, & Roder, 2004; Burton, McLaren, & Sinclair, 2006) provide insights into the brain reorganization and behavioral compensations that occur following sensory deprivation. Clear neuroplastic changes result from deafferentation of visual cortical areas through peripheral blindness, with the most striking finding being the activation of occipital cortex in response to auditory and tactile stimulation.

The possibility of neural recovery in adults, and also its importance, has inspired more and more studies exploring the mechanisms of learning at various levels, such as the behavioral, the cognitive and the neural. Around three decades ago, some studies (Ramachandran & Braddick, 1973; McKee & Westheimer, 1978; Fiorentini & Berardi, 1980) started to report the finding that observers' performance of cognitive or psychophysics tasks could be significantly improved after a certain period of practicing. Fiorentini and Berardi (1980) first pointed out the implications of these findings-- that they demonstrate the plasticity of human perceptual systems even in adults. Soon after, great enthusiasm was evoked within cognitive and perceptual fields, especially in visual research, about the functional characteristics and underlying mechanisms of this kind of perceptual learning.

Though the fact that performance improves along with the practice has been well noted and studied for long time, the phenomena of perceptual learning have triggered extensive interest and attention because they are different from traditional learning tasks in several critical aspects. Perceptual learning is the long-lasting improvement of perceptual recognition or discrimination ability resulting from repeated practice. Performance improvement, such as a decrease in threshold, usually happens without observers' awareness or beyond their voluntary controls. Perceptual learning does not only result from the changing of observers' task implementation strategies, but also involves changes happening in early stages of the relevant sensory modality. Studies on perceptual learning are very useful, as discussed by Zenger and Sagi (2002), because

“they can reveal new information, first, about the type of processing that underlies the visual system, and second, about the rules that govern plasticity of the system”. Neural plasticity revealed from perceptual learning in normal adult observers also has significant implications with regard to patients with perceptual system injuries.

1.2 Models and theories of perceptual learning

Along with the fruitful discoveries of learning phenomena, a variety of models and hypotheses of learning mechanisms have been proposed and tested, including cognitive and perceptual models, computational and noise theories and neural and synaptic hypotheses. Based on the finding of fast learning in visual hyperacuity, Poggio et al (1992) provided a hypothesis that rapid performance improvement could be obtained by synthesizing a small number of examples for a certain task, and they succeeded to build up a simple network to simulate the fast perceptual learning process. Goldstone (1998) proposed four possible mechanisms for perceptual learning: attention weighting, imprinting, differentiation and unitization. Information combination theory (van Ee, 2001) deals with the way to utilize information within or between modalities optimally, with the fundamental statement that the weighting of various information resources depends on the reliability of the signal. There are also quite a few studies focusing on probability theory exploring the relationship of Bayesian natural selection and the evolution of perceptual systems (Geisler & Diehl, 2002; Kersten, Mamassian, & Yuille, 2004). Another prominent hypothesis of perceptual learning is signal/noise theory (Doshier & Lu,

1998, 1999, 2006; Gold, Bennett, & Sekuler, 1999; Hurlbert, 2000; Sperling et al, 2005), which treats the individual perceptual mechanism as an active signal searching system, trying to extract proper signal from both internal noise and external noise. Therefore the relative amounts of internal and external noise regulate the neural response. Whether or not a neuron detects the signal depends on how well tuned it is to that particular signal, and on how easy the signal is to detect.

Although we could gain great benefits from cognitive, perceptual, and computational models and theories, there is argument that they are somewhat descriptive and phenomenal explanations, rather than neural mechanisms. So, neuronal and synaptic hypotheses have been developed trying to explore and interpret perceptual learning from the perspective of neural mechanisms. The early work was from Hebb (1949) who tried to build a bridge to connect behavior, brain function and cellular processing. He suggested that the strength or efficiency of connections between synapses increases if the firing of one always causes another one. Based on empirical studies, Hebb's synaptic connection theory was further elaborated and more neural and synaptic hypotheses were proposed. One well accepted one is the covariance hypothesis (Sejnowski, 1977; Fregnac et al, 1988), which claims that one mechanism underlying visual cortical plasticity is to modulate the synaptic transmission by temporal correlation between pre- and postsynaptic activities. Synaptic strength will increase if the pre-synaptic neuron repeatedly succeeds to trigger a postsynaptic neuron, while the synaptic strength will decrease if this triggering keeps on failing. Therefore, the covariance between pre- and

post-synaptic activities determines synaptic efficiency. Some recent studies (Qi et al, 2005) demonstrated the validity of such Pavlovian conditioning in a learning task of bistable visual appearance by cue recruitment, suggesting the significance of temporal connections in perceptual learning. A series of studies on task-irrelevant perceptual learning (Watanabe, 2001; Seitz & Watanabe, 2003; Seitz & Watanabe, 2005; Seitz et al, 2009) showed that task-irrelevant stimulus features can be learned as long as they are presented in a way temporally associated with task-relevant features. Perceptual learning can happen without perception or awareness if the visual stimuli are temporally paired with rewards and reinforcement. A unified model with association hypothesis for perceptual learning has been proposed to explain what is gating learning when attention is absent.

The proposal of anti-Hebbian learning rules suggests that the strength of synaptic connectivity can decrease after temporally paired neural firings through modifiable inhibitory feedback connections (Figure 1.1, Foldiak, 1990). In other words, input fibers fire together, but output fibers have no correlations. This decorrelation by anti-Hebbian mutual interactions is very useful to reduce the information redundancy and form sparse representations, which makes the system more sensitive to new appearing associations. An anti-Hebbian learning network can fairly interpret the after-effects of adaptation in the visual cortex (Barlow & Foldiak, 1989). Anti-Hebbian learning rules have been investigated and demonstrated widely in neurological studies, such as lateral inhibitory synaptic networks (Girolami & Fyfe, 1996).

Figure 1.1 The Architecture of a proposed learning network (adapted from Foldiak, 1990).

Empty circles represent Hebbian excitatory, filled circles represent anti-Hebbian inhibitory connections. The network has m inputs x , and n representation units y . In this network, the detection of suspicious coincidences is performed by conventional Hebbian feed-forward weights, but units are connected by anti-Hebbian inhibitory feedback connections.

1.3 Neural networks and inhibitory mechanism in perceptual learning

To construct feasible learning networks, interneurons, especially the ones with inhibitory functions, play critical roles. Researchers (Lowel & Singer, 1992; Lowel, 1994) obtaining findings more directly from neurophysiology proposed that horizontal long-range connections, which are functionally suitable for detecting contours, edges and etc, are possible candidates for perceptual learning due to their layout and postnatal high plasticity even after maturity. Cortical connectivity includes vertical intercortical connections clustered in function columns and horizontal intracortical long-range connections mainly constituting nonclassical receptive fields (Eysel & Schweigart, 1999).

Different from the classical receptive fields which are relatively individual, horizontal long-range connections have high integrative capabilities which are experience-dependent and important for context-dependent modifications. Perceptual learning could be at least partially attributed to the reorganization of networks built from these horizontal long-range connections, with a larger excitatory than inhibitory network. Results from optical recording of alert monkeys showed that horizontal connections and lateral interactions in visual cortex could be the substrates for spatial integration and cortical plasticity (Gilbert et al, 1996). Studies (Maffei, Nelson, & Turrigiano, 2004) suturing rats' eyes after their birth demonstrated that visual deprivation during the critical period could change the relations between excitatory and inhibitory neurons in layer 4 of V1, which is one of the potential mechanisms of perceptual plasticity at the neuron level. Further, Maffei et al (2006) studied the potentiation of cortical inhibition by visual deprivation. A major effect of visual deprivation between postnatal day 18 (P18) and P21 is a potentiation of feedback inhibition within layer 4, which occurs through a process like long-term potentiation of inhibition (LTPi). The results of visual deprivation during P14 to P17 and P18 to P21 are very different (almost opposite). Between P18 to P21, visual deprivation leaves excitatory connections in layer 4 unaffected, but potentiates inhibitory feedback between fast-spiking basket cells (inhibitory neurons) and star pyramidal neurons (excitatory neurons). Additionally, studies have shown that the inhibitory mechanism has a more critical role than the excitatory network in reconstructing mature cortex in adults (Hensch et al, 1998; Harauzov et al, 2010).

Despite numerous findings regarding interneurons and perceptual learning networks from neural cellular and molecular levels (Berardi et al, 2003; Wonders & Anderson, 2006), there is a big gap between these results and our understanding of behavioral changes. So it is important to cautiously integrate inferences from various neuroscience techniques and behavioral studies. Imaging studies (Hannula, Simons & Cohen, 2005), on the one hand, shed light on further explorations of this gap; on the other hand, we still need to design and conduct more rigorous behavioral experiments to illuminate future directions of work on perceptual learning. Zenger and Sagi (2002) used contrast-masking experiments to investigate properties of the perceptual filters and the plasticity of facilitation and suppression in low-level visual networks after learning. They proposed that changes in the suppression region (with positive slope) of the contrast discrimination function suggest decreases in inhibitory interactions during practice.

The binocular visual system is a good model for exploring both excitatory and inhibitory mechanisms. From an early binocular vision model at and above threshold (Legge, 1979; Legge & Foley, 1980; Foley & Legge, 1981; Legge, 1984a, 1984b), researchers assembled a series of psychological tests (e.g., binocular summation, superimposed masking) to explore monocular and binocular pathways and interactions, and tried to build a unified neuro-computational framework that can account for numerous visual phenomena (e.g., Grossberg, 1987; Ding & Sperling, 2006; Meese, Georgeson, & Baker, 2006; Baker & Meese, 2007, Huang et al, 2009). Among those, there are theories focusing specifically on binocular rivalry, including a two-stage

competitive neural model (Wolfe, 1986; Lehky, 1988; Blake, 1989; Lehky & Blake, 1991; Wilson, Blake, & Lee, 2001) along with computational evidence (Wilson, 2003). Our current project mainly employs the paradigm of binocular rivalry, as it is largely based on an interocular inhibitory mechanism whose plasticity we are interested in. For example, Figure 1.2 plots a schematic neural circuit for binocular rivalry adapted from Lehky's model (1988). He proposed a network of rivalry involving reciprocal feedback inhibition between monocular signals, prior to the point of binocular convergence, so that it can simulate the temporal dynamics of rivalry and monocular predominance related to unilateral stimulus strength. If one monocular channel gets stronger input signals than the other one, the inhibitory mechanism will be activated to suppress the weaker input signals from the other side, and rivalry occurs due to the adaptation of the inhibitory feedback. When the two monocular channels get highly correlated input signals, the inhibitory effect between them gets weaker so that fusion can be allowed in his model. Although the importance of binocular vision has been long acknowledged and studied (Howard & Rogers, 1995; Alais & Blake, 2005), there is not much research investigating perceptual learning on binocular interactions and underlying mechanisms. This dissertation capitalizes on these properties of the binocular visual system to investigate the perceptual learning of binocular interactions.

The goal of the current project is to investigate the plasticity of binocular interactions and to understand this plasticity's underlying mechanisms. Our specific questions are: does interocular imbalance vary across the retina, and does it relate to other monocular or

binocular functions? Can interocular imbalance be changed by perceptual learning, and if so what is the most efficient protocol? What is the role of attention in perceptual learning of interocular imbalance? What do boundary contours contribute to perceptual learning? How can we generalize the learning effects? How does perceptual learning influence the process of binocular summation?

Figure 1.2 Example of a neural network model of binocular rivalry (adapted from Lehky, 1988). Reciprocal inhibition occurs between left-eye and right-eye neurons as a result of inhibitory interneuronal connections. Competitive interactions happen prior to binocular combination.

CHAPTER 2

EXPERIMENT 1: MEASURING LOCAL SENSORY EYE DOMINANCE

2.1 Rationale

When corresponding retinal areas receive different images, such as orthogonal gratings, the interocular inhibitory mechanism is responsible for binocular suppression. In the normal binocular visual system, the interocular inhibition between the two eyes is expected to be balanced. Sensory eye dominance (SED), also called interocular imbalance, refers to one eye having a competitive advantage over the fellow eye when viewing a pair of binocular rivalry stimuli with equal strength. It has been shown that sensory dominance and motor dominance do not necessarily reside in the same eye, and observers with larger SED tend to take longer time to perceive depth in simple stereograms (Coren & Kaplan, 1973; Porac & Coren, 1976; Weinman & Cooke, 1982). In a previous study, Ooi & He (2001) measured the global interocular imbalance using six pairs of rivalry gratings. Observers reported the overall dominant percept; for example, seeing more red or green gratings. The intensity difference between the gratings in the two eyes required to achieve equal predominance is defined as the interocular imbalance. Thus, if the right eye (RE) requires higher intensity gratings to achieve equal

predominance, the RE is called the weak eye, and the left eye (LE) is the sensory dominant eye.

The goal of the current experiment is to investigate the local sensory eye dominance at various retinal locations, and its relationship with contrast sensitivity and stereopsis ability. We focused on the following three specific questions: First, does the local interocular imbalance vary across the retina? Second, can the local interocular imbalance be attributed to the interocular contrast threshold difference? Third, does the local interocular imbalance impede stereopsis? To answer these questions, we conducted a series of measures of local interocular imbalance (i.e., SED), interocular contrast threshold difference, stereo disparity threshold, and stereo reaction time at 17 retinal locations (Figure 2.1, note that all stimuli are well within the location of the optic disk, i.e., $\sim 15^\circ$ eccentricity). A pair of dichoptic vertical and horizontal gratings is used to measure SED. The vertical grating has a fixed contrast, and is presented, for example, to the left eye (LE) first (Figure 2.2a). The contrast of the horizontal grating in the right eye (RE) is adjusted using a QUEST procedure for the observer to achieve equal predominance. We refer to this contrast as the RE balance contrast. We then switch the gratings between the two eyes (Figure 2.2b) to measure the LE balance contrast. SED is the difference between the LE and RE balance contrast values, and a positive value indicates right eye dominance.

Figure 2.1 Seventeen retinal locations measured in the current study. The stimulus size from fovea to 4° eccentricity was scaled according to the cortical magnification factor.

2.2 Hypotheses

Our first hypothesis is that interocular inhibition and interactions, which result in SED, more likely occur in primary visual cortex, where the majority of monocular neurons that carry the eye-of-origin information are found (Blake et al, 1980; Maunsell & Van Essen, 1983; Ooi & He, 1999). Accordingly, one characteristic of SED should be the specificity of retinal location, and we predicted that SEDs are heterogeneous across retina area.

Secondly, we hypothesized that it is an interocular inhibitory mechanism that is responsible for SED. SED manifests as an unequal mutual inhibition between the two ocular channels, which can be revealed when two dissimilar dichoptic images with equal physical strength are presented, triggering the interocular inhibitory mechanism to suppress one of the two images (Ooi & He, 2001). Thus, SED is not simply an additive result of monocular functions, such as the interocular difference in monocular contrast sensitivity.

Thirdly, since interocular inhibition is an integral part of binocular visual processing, we hypothesized that SED should correlate with other binocular visual functions. As equal mutual interocular inhibition is required for efficient processing of binocular information, excessive SED can reduce stereo acuity and slow down stereo processing (Wolfe, 1986; Schor, 1991). Therefore, we predicted that higher stereo disparity threshold and longer stereo reaction time would be recorded at retinal locations with larger SED.

2.3 Methods

2.3.1 Design

A Macintosh G4 computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 19-inch Mitsubishi flat screen CRT monitor with resolution of 1280 x 1024 at 100 Hz refresh rate (except for stereopsis test: 2048 x 1536 at 75 Hz). All observers (one author and eleven naïve observers giving informed

consent) had normal binocular vision. We measured the local interocular imbalance (SED), interocular contrast threshold difference, stereo disparity threshold, and stereo reaction time at 17 retinal locations (Figure 2.1). Additionally, we measured motor eye dominance and binocular competition at fovea (ten out of twelve observers performed this task).

2.3.2 Observers

All twelve observers (ages 21-29) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 40 arc sec), and passed the Keystone vision-screening test. During the experiments they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

2.3.3 Stimuli and procedure

Interocular imbalance test to measure SED at 17 retinal locations

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (mean 35 cd/m^2) with a gray background ($11^\circ \times 11^\circ$, 35 cd/m^2) (Figure 2.2a-b). The contrast of the vertical grating was fixed (1.5 log units) while the contrast of the horizontal grating was varied (0-1.99 log units). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width = 0.1° , 70 cd/m^2) and the presentation of the dichoptic orthogonal gratings (500 msec), followed by a 200 msec mask ($11^\circ \times 11^\circ$

checkerboard sinusoidal grating, 35 cd/m², 1.5 log units). The observer responded to his/her percept by key presses (1=vertical, 2=horizontal). If a mixture of vertical and horizontal orientation was seen, the observer would respond to the predominant orientation. The horizontal grating contrast was adjusted after each trial until equal predominance was achieved using the QUEST procedure (50 trials/block). When the horizontal grating was presented to the LE we refer to its contrast at equal predominance as the LE's balance contrast. Then the gratings were switched between the eyes to obtain the RE's balance contrast. Their difference is defined as SED.

SED was measured at 17 retinal locations, including fovea and the eccentricities of 2° and 4° with eight concentric locations respectively (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°). When grating discs were presented in fovea, the spatial frequency was 5 cpd, and the size was 0.75°. The spatial frequency and disc size were scaled proportionally for peripheral presentation according to the cortical magnification factor given by the formula: target frequency (cpd) = foveal frequency / [1 + eccentricity (°) / 3]; target size (°) = foveal size * [1 + eccentricity (°) / 3] (Rovamo and Virsu, 1979). Accordingly, [3 cpd, 1.25°] were used for the grating at 2° eccentricity, and [2.14 cpd, 1.75°] were used for the grating at 4° eccentricity. The spatial frequency of mask was consistent with the grating disc. Thus, a total of 34 stimulus combinations (17 locations x 2 eyes), in a randomized testing order, were run twice. Extra blocks were performed if the two repeats data were not consistent with each other (difference was larger than 0.05 log units).

Figure 2.2 (a) Stimulus for measuring RE's balance contrast, which is referred as the contrast of horizontal grating at equal predominance while the contrast of the vertical grating was fixed at 1.5 log units. (b) Stimulus for measuring LE's balance contrast. The difference between the contrasts obtained from (a) and (b) is defined as SED. (c) Stimulus for measuring dynamics of interocular dominance and suppression at fovea. (d) The 2AFC stimulus presentation sequence for testing monocular contrast threshold.

Monocular contrast threshold at 17 retinal locations

The monocular sinusoidal grating (35 cd/m^2 , 500 msec) was either horizontal or vertical for the contrast sensitivity test. The fellow eye viewed a homogeneous field. The test was conducted using a 2AFC method in combination with the QUEST procedure. As shown in Figure 2.2d, the 2AFC stimulus presentation sequence was: fixation, interval-1 (500 msec), blank (400 msec), interval-2 (500 msec), blank (400 msec), and mask ($11^\circ \times 11^\circ$ checkerboard sinusoidal grating, 35 cd/m^2 , 1.5 log units contrast, 200 msec). The grating was presented at only one interval while the other interval had a blank field. The observer responded to seeing the grating either in interval-1 or -2 by key press, and audio feedback was given. The grating contrast was adjusted after each trial (by QUEST) to obtain the threshold. Monocular contrast threshold was measured at the same 17 retinal locations as described in the SED test, with the scaled grating spatial frequency and disc size used at each eccentricity (fovea: 5 cpd, 0.75° ; 2° : 3 cpd, 1.25° ; 4° : 2.14 cpd, 1.75°). Thus, a total of 68 stimulus combinations (17 locations x 2 eyes x 2 orientations), in a randomized testing order, were run. Each stimulus combination was repeated over 2 blocks of trials (50 trials/block). Extra blocks were performed if the two repeats data were not consistent with each other (difference was larger than 0.05 log units).

Stereo threshold and reaction time at 17 retinal locations

An $11^\circ \times 11^\circ$ random-dot stereogram (dot size= 0.0132° , 35 cd/m^2 , 1.5 log units contrast) with a variable crossed-disparity disc target was used (fovea: 0.75° ; 2° : 1.25° ; 4° : 1.75°). We used the standard 2AFC method in combination with the staircase procedure

to measure stereo disparity threshold (Figure 2.3a). The temporal sequence of stimulus presentation was fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and random-dot mask (200 msec, $11^\circ \times 11^\circ$, 35cd/m^2). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~50-60 trials), and the average of the last 8 reversals were taken as the threshold. Stereo threshold was measured at the same 17 retinal locations as described in the SED test, in a randomized testing order. Each block was repeated twice, and extra blocks were performed if the two repeats data were not consistent with each other (difference was larger than 0.5 minutes).

To measure stereo reaction time, the binocular disparity of the stereo disc was either ± 6 arc min (Figure 2.3b). The observer pressed a key immediately upon detecting the stereo disc (1=front, 2=back), and the stimulus was removed. A blank screen (400 msec), followed by a mask (200 msec), ended the trial, and audio feedback was given. If depth was not detected, the stimulus timed-out after 2500 msec. Each block consisted of 60 trials, with 30 front-trials and 30 back-trials, and three 60-trial blocks were tested. The average reaction times of the front and back trials were taken as the final results. All reaction times with the correct responses were longer than 100 msec. The observers were instructed that accuracy is desired above speed, through this task is to measure reaction time. And all observers' accuracy was higher than the criteria of 70%. Stereo reaction time was also measured at these 17 retinal locations in a randomized testing order.

Figure 2.3 Stimuli and presentation sequence for stereo tests. (a) The 2AFC stimulus presentation sequence for testing stereo threshold. (b) The stimulus presentation sequence for testing stereo reaction times.

Binocular competition at fovea

The stimulus comprised a pair of dichoptic vertical and horizontal grating discs (1° , 5 cpd, 35 cd/m^2 , 1.99 log units contrast) surrounded by a $7.5^\circ \times 7.5^\circ$ gray square (35 cd/m^2)

(Figure 2.2c). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) and the presentation of the dichoptic orthogonal gratings (30 sec), followed by a 1 sec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.99 log units contrast). The observer's task was to report (track) his/her instantaneous percept of the binocular competitive stimulus over the 30 sec stimulus presentation. Depending on the percept, vertical, horizontal, or a mixture of both, he/she would depress the appropriate key until the next percept took over. The predominance (sum of dominance duration/ total tracking duration) of seeing each percept was calculated. We also tested the stimulus combination with the vertical and horizontal gratings switched between eyes. Both combinations were repeated 4 times, with randomized order.

Motor eye dominance

A variation of the Ring sighting test was used (Borish, 1970). The observer was instructed to bring both hands simultaneously to the front of his/her face at arms length, and to form a ring (2-3 inches in diameter) by bringing together the index finger and thumb from each hand. Then the observer was asked to sight a target with both eyes open through this "ring", making sure the target was placed in the center of the ring. After this, he/she was asked to close each eye alternately, and to determine whether the right or left eye saw the target as more centered in the ring. The eye that saw the target as more centered was defined as the motor-dominant eye.

2.4 Results

1) The interocular imbalance (SED) varies with retinal location in both sign and magnitude.

As presented in Figure 2.4a, we used a color spectrum from red to green to indicate the degree of eye dominance from right to left eye; yellow indicates no interocular imbalance. Results from 12 observers show that both the sign (right or left eye) and magnitude of the local SED vary with test location, indicating that the local SED is retinal location specific. For some observers (e.g., S10), SED is locally heterogeneous in both sign and magnitude; and for some observers (e.g., S4), SED is globally dominant in one eye.

(a) SED

(b) Interocular contrast threshold difference

Figure 2.4 Results of measuring local (a) SED and (b) interocular contrast threshold difference at 17 retinal locations from 12 observers. A color spectrum from red to green is used to indicate the degree of eye dominant from right to left eye. Yellow indicates no interocular imbalance. This figure demonstrates that both (a) SED and (b) interocular contrast threshold difference vary with retinal location in both sign and magnitude.

We also analyzed the relationships between SEDs at different eccentricities, i.e., fovea, 2°, and 4°, as plotted in Figure 2.5. Results show that the foveal SED is highly correlated to the average SED at 2° eccentricity ($r=0.852$, $p<0.001$, Figure 2.5a), and the average SED at 4° eccentricity ($r=0.711$, $p=0.010$, Figure 2.5b). For the same local angle (e.g., 135°), SEDs at 2° and 4° eccentricities are strongly correlated ($r=0.615$, $p<0.001$, Figure 2.5c); as well as the average SED at 2° and 4° eccentricities ($r=0.856$, $p<0.001$, Figure 2.5d). Furthermore, there is a strong correlation between the foveal SED and parafoveal SED (averaged from locations at 2° and 4° eccentricities) ($r=0.818$, $p=0.001$, Figure 2.5e), and a strong correlation between the foveal SED and the average SED from all 17 retinal locations tested ($r=0.941$, $p<0.001$, Figure 2.5f). Therefore, despite the inhomogeneity of the local interocular imbalance, the foveal interocular imbalance is a reliable predictor of the global interocular imbalance.

Figure 2.5 A high correlation between (a) foveal SED and average SED at 2° eccentricity; (b) foveal SED and average SED at 4° eccentricity; (c) SEDs at 2° and 4° eccentricities for the same local angle (e.g., 135°); (d) average SED at 2° and 4° eccentricities; (e) foveal

SED and parafoveal SED (averaged from locations at 2° and 4° eccentricities); (f) foveal SED and global SED (the average SED from all 17 retinal locations tested).

Additionally, we investigated the relationships between sensory eye dominance, motor eye dominance, and interocular difference in predominance of binocular competition. As shown in Figure 2.6a, sensory dominance and motor dominance do not necessarily reside in the same eye. Ten out of twelve observers also carried out the task of binocular competition at fovea, and we calculated their interocular difference in predominance as $\text{Predominance(RE, H)} - \text{Predominance(LE, H)} + \text{Predominance(RE, V)} - \text{Predominance(LE, V)}$. Positive values indicate a more dominant right eye in the binocular competition. We found a high correlation between the SED at fovea and the interocular difference in predominance ($r=0.892, p=0.001$).

Figure 2.6 Relationships between SED at fovea, motor eye dominance, and interocular difference in predominance of binocular competition. (a) Sensory dominance and motor

dominance do not necessarily reside in the same eye. (b) SED at fovea is highly correlated with the interocular difference in predominance.

2) An interocular contrast threshold difference can not fully account for SED.

Secondly, we measured the local monocular contrast threshold in each eye with both vertical and horizontal orientations at 17 retinal locations. Then we calculated the interocular contrast threshold difference as $\text{Threshold(LE, H)} - \text{Threshold(RE, H)} + \text{Threshold(LE, V)} - \text{Threshold(RE, V)}$. Positive values indicate a more sensitive right eye. Results for each observer are plotted in Figure 2.4b using different colors to indicate which eye is more sensitive: red indicates a more sensitive right eye, and green indicates a more sensitive left eye. It is shown that observer's interocular contrast threshold difference varies with retinal location in both sign and magnitude. Then we analyzed the relationship between SED and interocular contrast threshold difference. We found that for some observers, SED and interocular contrast threshold difference are more or less consistent with each other (e.g., S7), while for some observers, SED and interocular contrast threshold difference are inconsistent (e.g., S4).

Further analysis showed that there is a moderate correlation between interocular contrast threshold difference and SED ($r=0.441$, $p<0.001$, Figure 2.7a). As shown in Figure 2.7b-d, the correlations vary across different eccentricities (fovea: $r=0.782$, $p=0.003$; 2° : $r=0.490$, $p<0.001$; 4° : $r=0.316$, $p=0.002$), with a decrease towards parafovea. But overall, an interocular contrast threshold difference cannot be the sole cause of SED.

Figure 2.7 Moderate correlations between interocular contrast threshold difference and SED (a) overall; (b) at fovea; (c) at 2° eccentricity; (d) at 4° eccentricity.

3) SED has a significant impact on both stereo disparity threshold and reaction time.

Thirdly, we measured the stereo disparity threshold and stereo reaction time at 17 retinal locations with the random-dot stereogram, and each observer's data were plotted respectively in figure 2.8 according to a gray scale. The overall data patterns also show inhomogeneity across the visual field.

(a) Binocular disparity threshold

(b) Stereo reaction time

Figure 2.8 Results of measuring local (a) binocular disparity threshold and (b) reaction time to detect binocular depth at 17 retinal locations from 12 observers. We used a gray scale to indicate the magnitude. The overall patterns also show both measurements vary with retinal location.

We then analyzed the correlation between stereo disparity threshold and SED, and the correlation between stereo disparity threshold and interocular contrast threshold difference. As we used sign to indicate eye dominance for SED, and eye sensitivity for interocular contrast threshold difference, here we applied the absolute values for both measurements in further analysis. There is a significant correlation between SED and stereo disparity threshold ($r=0.464$, $p<0.001$, Figure 2.9a), with a variance across different eccentricities (fovea: $r=0.733$, $p=0.007$; 2° : $r=0.547$, $p<0.001$; 4° : $r=0.471$, $p<0.001$, Figure 2.9b-d).

Figure 2.9 Significant correlations between SED and stereo disparity threshold (a) overall; (b) at fovea; (c) at 2° eccentricity; (d) at 4° eccentricity.

On the other hand, the correlation between the interocular contrast threshold difference and stereo disparity threshold is not significant ($r=0.097$, $p=0.166$, Figure 2.10a), with a variance across different eccentricities (fovea: $r=0.503$, $p=0.096$; 2°: $r=0.142$, $p=0.166$; 4°: $r=0.184$, $p=0.073$, Figure 2.10b-d). Overall, interocular imbalance and stereo disparity threshold have higher correlations than interocular contrast threshold difference and stereo disparity threshold.

Figure 2.10 Low correlations between interocular contrast threshold difference and stereo disparity threshold (a) overall; (b) at fovea; (c) at 2° eccentricity; (d) at 4° eccentricity.

Then we analyzed the correlation between stereo reaction time and interocular imbalance, and the correlation between stereo reaction time and interocular contrast threshold difference. Because of the large variability in reaction time across observers, we used z scores of reaction time for our analysis. Results showed that there is a significant correlation between SED and the relative stereo reaction time. ($r=0.442$,

$p < 0.001$, Figure 2.11a), with a variance across different eccentricities (fovea: $r = 0.497$, $p = 0.100$; 2° : $r = 0.401$, $p < 0.001$; 4° : $r = 0.502$, $p < 0.001$, Figure 2.11b-d).

Figure 2.11 Significant correlations between SED and relative reaction time (z score) (a) overall; (b) at fovea; (c) at 2° eccentricity; (d) at 4° eccentricity.

In contrast, the correlation between the interocular contrast threshold difference and the relative stereo reaction time is not significant ($r = -0.025$, $p = 0.727$, Figure 2.12a), with a variance across different eccentricities (fovea: $r = 0.013$, $p = 0.969$; 2° : $r = -0.105$, $p = 0.310$; 4° : $r = 0.124$, $p = 0.230$, Figure 2.12b-d). Overall, interocular imbalance and stereo reaction

time have higher correlations than interocular contrast threshold difference and stereo reaction time.

Figure 2.12 Low correlations between interocular contrast threshold difference and relative reaction time (z score) (a) overall; (b) at fovea; (c) at 2° eccentricity; (d) at 4° eccentricity.

Therefore, both the stereo threshold and reaction time tend to increase with the magnitude of the local SED, suggesting that SED can impede stereo processing. Further

analysis using linear regression model shows that SED has a significant impact on stereo disparity threshold and stereo reaction time; the impact of interocular contrast threshold difference is less.

$$\text{Disparity Threshold} = 1.805 + 4.764 \cdot \text{SED} - 0.509 \cdot \text{Contrast Threshold}$$

$$[R^2=0.217, F(2,201)=27.811, p<0.001;$$

$$\text{SED: } \beta=0.476, t(201)=7.293, p<0.001;$$

$$\text{Contrast Threshold: } \beta=-0.040, t(201)=-0.614, p=0.540.]$$

$$\text{Reaction Time} = -0.442 + 2.830 \cdot \text{SED} - 1.216 \cdot \text{Contrast Threshold}$$

$$[R^2=0.221, F(2,201)=28.532, p<0.001;$$

$$\text{SED: } \beta=0.490, t(201)=7.544, p<0.001;$$

$$\text{Contrast Threshold: } \beta=-0.166, t(201)=-2.557, p=0.011.]$$

2.5 Discussion

Our finding that sensory eye dominance is retinal location specific strongly supports our hypothesis that interocular inhibitory mechanism underlies early visual networks. Nevertheless, the foveal SED can be a reliable predictor of the overall sensory eye dominance (within 4° eccentricity). We further demonstrated that SED involves processing related to binocular functions by assessing its relationships with the monocular contrast threshold and stereopsis perception. An interocular contrast threshold difference, which also varies with retinal location, cannot be the sole cause of SED, i.e., interocular imbalance. More importantly, SED can significantly impede both stereo

disparity acuity and stereo reaction speed, whereas interocular contrast threshold difference has a smaller impact. Therefore, we propose that stereopsis ability should be improved if excessive SED can be decreased by perceptual learning. Given the importance of reducing SED, a design of an effective training protocol is urged, which could be potentially applied to clinical treatment.

A study on how to effectively reduce SED in adults through visual training has important theoretical implications for neuroscience and vision research. For example, since the SED is a manifestation of an unbalanced interocular inhibitory mechanism, it can be used as a model to investigate adult neural plasticity of the inhibitory cortical network and its impact on behavior (Hensch et al, 1998; Huang et al, 1999; Karmarkar & Dan, 2006; Harauzov et al, 2010). Moreover, the clinical condition of amblyopia can be considered as an extreme case of SED, where the amblyopic eye receives an unbalanced amount of interocular inhibition. Consequently, reducing an amblyopic patient's SED can be an important part of amblyopia therapy, given its potential for improving binocular visual functions.

2.6 Summary

By measuring local SED, contrast sensitivity, and stereo ability, we found that: 1) Within a 4 deg retinal eccentricity, interocular imbalance is local and retinal location specific. The fovea's interocular imbalance is strongly correlated with the average interocular imbalance. 2) The local interocular imbalance can not be entirely attributed to

a difference in interocular contrast threshold. 3) Both disparity threshold and reaction time increase with the magnitude of the interocular imbalance. This suggests that interocular imbalance can impede stereo processing. 4) By applying the linear regression model, we found that compared to interocular contrast threshold difference, interocular imbalance has a stronger impact on stereo processing.

CHAPTER 3

EXPERIMENT 2: PERCEPTUAL LEARNING OF INTEROCULAR IMBALANCE

3.1 Rationale and theoretical neural model

Flourishing studies of perceptual learning, especially in the field of vision science, have revealed the presence of continuous sensory cortical plasticity in adults (Karni & Sagi, 1991; Sugita, 1996; Doshier & Lu, 1999; Crist, Li, & Gilbert, 2001). From the clinical perspective, studies have demonstrated perceptual learning as an effective means to improve the monocular visual ability of amblyopic adults (Levi & Li, 2009 mini-review). Perceptual learning as the new behavioral treatment for amblyopia is more desirable than the traditional patching therapy, since the latter is more time consuming and induces low self-esteem for the patient who is wearing it daily.

Meanwhile, neurophysiological studies (Gilbert et al, 1996; Maffei, Nelson, & Turrigiano, 2004; Maffei et al, 2006) have suggested that one potential neural mechanism underlying perceptual learning is to modify excitatory and inhibitory networks through extensive training. Furthermore, inhibitory networks have been found to be especially important for neural plasticity in adults, because they are more dynamic than excitatory

networks in mature cortex (Hensch et al, 1998; Karmarkar & Dan, 2006; Harauzov et al, 2010). Research on inhibitory interneurons has reached down to neural cellular and molecular levels (Berardi et al, 2003; Wonders & Anderson, 2006). However, most visual psychophysics studies on perceptual learning tend not to differentiate the functions and mechanisms underlying excitatory and inhibitory networks. Therefore, behavioral experiments addressing the inhibitory networks explicitly are needed, and are expected to have more clinical implications in facilitating cortical plasticity in adults.

As discussed in the last chapter, large sensory eye dominance (SED), or interocular imbalance, is induced by unbalanced interocular inhibition, and can impede stereo functions (Schor, 1991, Ooi & He, 2001). Our goal is to design a perceptual learning approach to reduce SED by tackling the inhibitory mechanism especially. The binocular visual system provides a good model to study the interactions between two inputs and how they shape the visual cortex with both excitatory and inhibitory networks (Wiesel & Hubel, 1963). Figure 3.1a presents a simplified two-level neural model of binocular interactions proposed by Wilson (2003). At the lower level, monocular neurons with different orientation preference from each eye inhibit one another. At the higher level, monocular neurons from each eye with the same orientation preference converge. These higher-level neurons are also involved in competitive inhibitory interactions. Interocular inhibition is activated when the two eyes are stimulated with a pair of orthogonal gratings. In normally developed adults, the mutual inhibition between neurons of the two eyes is largely balanced. But when the mutual inhibition is unbalanced, SED will occur to

different extent, even for people with normal visual acuity. Binocular vision can be impaired by large SED, whose extreme case is speculated to be amblyopia, a developmental malfunction resulting from abnormal binocular visual experience during early life (Levi, 1994). Figure 3.1b conceptualizes an example in which the inhibition from the right eye (RE) on the left eye (LE) is much stronger. Thereby when stimulated by two orthogonal gratings with the same contrast, the signals in the left eye's channel (vertical grating) are suppressed and only signals in the right eye's channel (horizontal grating) can travel upstream, which leads to the perception of only the horizontal grating.

Figure 3.1 A conceptual two-level neural model of binocular interaction (adapted from Wilson, 2003). (a) At the lower level, monocular neurons with preference of orthogonal orientations mutually inhibit each other; and at the higher level, inputs of cortical neurons with common orientation preference from the two eyes converge. (b) SED with strong inhibition on the LE. When orthogonal gratings with equal contrast are presented to the

two eyes, the RE's grating (strong eye) is perceived while the LE's grating (weak eye) is suppressed, due to the stronger inhibition on the LE's monocular neurons.

The method we use to quantify SED is the same as the one described in Chapter 2. Take the case in Figure 3.2a for example. We present dichoptic vertical and horizontal gratings to the two eyes, with the contrast of LE's vertical grating fixed. The observer adjusts the contrast of the RE's horizontal grating until he/she has an equal chance of perceiving either grating. We refer to this contrast as the RE *balance contrast*. Then the gratings in the two eyes are switched (Figure 3.2b) to obtain the LE balance contrast. Since the same vertical grating is used, we define the difference between the two balance contrast values as the SED. The eye with the higher balance contrast is the weak eye.

Figure 3.2 Stimuli for measuring SED. (a) and (b) Orthogonal gratings used to measure the balance contrast in the RE (a) and LE (b), whose difference defines the SED.

In order to reduce SED, as in most perceptual leaning paradigms, training would mainly focus on stimulating the weak eye and facilitating its excitatory network (Li & Levi 2004; Polat et al, 2004; Huang et al, 2007). We adopted this standard push-only

training protocol, in which only the weak eye is trained on an orientation discrimination task (push) while the strong eye is presented with a gray blank field (comparable to the traditional patching therapy for amblyopia). In contrast to the standard approach, we designed a novel push-pull training protocol that simultaneously taps both excitatory and inhibitory networks, with the emphasis on the plasticity of inhibitory synapses. During the training, dichoptic orthogonal gratings are presented to the two eyes, while a preceding rectangular frame, acting as an attention cue, is presented to the weak eye only (Ooi & He, 1999). The preceding cue activates transient attention to induce the weak eye's grating to be further processed (push) while the strong eye's grating is suppressed (pull). Of significance, the extra "pull" component of the push-pull training protocol stimulates the strong eye while denying its retinal image from being perceived. The observer is trained on an orientation discrimination task based on perception from his/her weak eye, though physical stimuli are presented to the both eyes. We predicted that the push-pull training protocol would be more efficient than the push-only training protocol in reducing SED and improving binocular vision, as well as theoretically revealing.

3.2 Hypotheses

Under the push-pull training protocol, the stimulus in the weak eye is always perceived due to the activation by the preceding cue, while the stimulus in the strong eye is always suppressed. According to the Hebbian and anti-Hebbian rules, we hypothesized that repeated suppression of the signals in the strong eye by the weak eye's inhibitory

inputs would enhance the efficacy of the weak eye's inhibitory synapses, as well as reduce the efficacy of the strong eye's inhibitory synapses. It may also have a secondary effect of enhancing the efficacy of the weak eye's excitatory synapses by repeatedly stimulating the weak eye to perceive its signals, while reducing the efficacy of the strong eye's excitatory synapses. As a result, the interocular imbalance, i.e., SED, should be reduced after training. As comparison, under the push-only training protocol, there is no inhibition from the weak eye on the strong eye, and the only possible change is the increasing efficacy of weak eye's excitatory synapses. So the SED is expected to have less reduction if any after training.

Second, we hypothesized that the change of interocular inhibition happens in early visual processing so that learning effects are stimulus specific and location specific. We predicted that SED would not reduce when it is tested with different pairs of gratings from the one used in training, or at other retinal locations than the training one. Moreover, we expected that the learning effect of SED reduction would last for a long period after the training stops (over weeks or even months), due to the changes in low-level visual neural networks.

Third, since the monocular excitatory synapses of the weak eye are stimulated in both push-pull and push-only protocols, we predicted that the weak eye's contrast detection threshold and orientation discrimination threshold would decrease on the trained orientation afterwards. However, general improvements of these two tasks are

also expected since it has been demonstrated that high-level visual processing is also involved in perceptual learning (Ahissar & Hochstein, 1993; Xiao et al, 2008).

Fourth, we predicted that binocular functions, e.g., stereopsis, would be improved along with the reduction of SED, and the improvement would be larger under the push-pull training protocol.

3.3 Methods

3.3.1 Design

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 21-inch Samsung SyncMaster flat screen CRT monitor with resolution of 1280 x 1024 at 100 Hz refresh rate (except for stereo threshold test: 2048 x 1536 at 75 Hz). All observers (one author and nine naïve observers giving informed consent) had normal binocular vision. We first measured SED with vertical and horizontal grating discs at eight concentric retinal locations 2° from the fovea. Two locations with the largest SED were chosen for the training.

Seven naïve observers were trained in an interleaved procedure, in which both push-pull (Figure 3.3a) and push-only (Figure 3.3b) protocols were implemented on the same day, over a 10-day period. During the training phase, these two training protocols were assigned to two retinal locations respectively. To accomplish this, each observer came to the laboratory for a one-hour morning session and a one-hour afternoon session (12 blocks/session) for a total of 10 days. The sequence of selecting the training protocol

(push-pull versus push-only) for each session was interleaved and counterbalanced with an ABBA within-subject design. To monitor the learning progress, we measured the observer's balance contrast before each morning's training session, and after each afternoon's training session. To further assess the learning effect, we ran three sets of tests in the pre- and post-training phase: (a) SED with 45° and 135° grating discs; (b) monocular contrast thresholds and orientation discrimination thresholds with vertical and horizontal grating discs; (c) stereo threshold and reaction time. For the stereo tests, an untrained location with the least SED was also measured. All seven observers participated in these three sets of tests, except for the untrained location condition in the third set of tests ($n = 5$). Additionally, SED with horizontal and vertical gratings was measured before and after the training at locations ($\pm 45^\circ$) adjacent to the two training locations and tested on all seven observers.

Separately, three other observers were trained with the push-pull protocol for 10 days, followed by the push-only protocol for a subsequent 10 days (sequential procedure). They received one hour of training during each daily session, and were only assessed for the learning effect on SED.

3.3.2 Observers

All ten adult observers (age 24-32) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 40 arc sec), and passed the Keystone vision screening tests. During the

experiments they viewed the monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm. For the observers who had never attended any psychophysical experiment before, we gave them one session practice of basic psychophysical tasks in fovea, including typical binocular rivalry, contrast sensitivity, and orientation discrimination, in order to stabilize their performance.

3.3.3 Stimuli and procedure

Interocular imbalance test to measure SED at 8 retinal locations

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2) (figure 3.2). The contrast of one grating was fixed (1.5 log units) while the other varied (0-1.99 log units). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) and the presentation of the dichoptic orthogonal gratings (500 msec), followed by a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units). The observer responded to his/her percept by key presses (1=vertical, 2=horizontal). The horizontal grating contrast was adjusted after each trial until equal predominance was achieved using the QUEST procedure (50 trials/block). When the horizontal grating was presented to the LE we refer to its contrast at equal predominance as the LE's balance contrast. Then the gratings were switched between the eyes to obtain the RE's balance contrast. Their difference is defined as SED.

In the pre-training phase, SED was measured at eight concentric retinal locations (0° , 45° , 90° , 135° , 180° , 225° , 270° , and 315°) 2° from the fovea. Two locations with the largest SED were chosen for the training. SED at the two training-locations was further tested with: (i) 45° and 135° orthogonal gratings; (ii) the method of constant stimuli instead of the QUEST procedure. One grating (e.g., vertical) contrast was fixed at 1.5 log units, while the other (horizontal) adopted one of seven levels (1.2-1.8 log units). Each trial was repeated 7 times/block over 6 blocks. These two measures were performed again in the post-training phase. Separately, SED was measured at four locations ($\pm 45^\circ$) adjacent to the trained-locations after the training. During the training-phase, the SED at the two training-locations were measured with horizontal/vertical gratings before and after each day's training session using the QUEST procedure.

The push-pull training protocol

A trial began with fixation at the nonius target and the presentation of an attention cue ($1.25^\circ \times 1.25^\circ$ frame with dash outline, width= 0.1° , 1.52 log units, 70 cd/m^2) for 100 msec (Figure 3.3a). After a 100 msec cue-lead-time, the first dichoptic gratings (500 msec, 1.25° , 3cpd, 35 cd/m^2) were presented. The same 100 msec cue was presented again 400 msec later, followed by a 100 msec cue-lead-time, and the second dichoptic gratings with a slightly different orientation in the weak eye (500 msec). Four hundred msec later, a 200 msec checkerboard sinusoidal grating mask ($7.5^\circ \times 7.5^\circ$, 3 cpd, 35 cd/m^2 , 1.5 log units) terminated the trial. The contrast values of the dichoptic gratings were those

that led to equal predominance with the interocular imbalance test. The observer reported by key press whether the first or second grating had the slight counterclockwise orientation, and audio feedback was given. Before the proper training, we determined for each observer that the cue successfully suppressed the grating viewed by the strong eye. The orientation discrimination threshold was obtained using the QUEST procedure. Twelve blocks (50 trials/block) were performed for each hour of training.

The push-only training protocol

The procedure was identical to the push-pull protocol with one important exception (Figure 3.3b). Instead of presenting a pair of dichoptic gratings to the training location, only a monocular grating is presented to the weak eye's training location while the corresponding location in the strong eye had a homogeneous gray (blank) field.

Figure 3.3 (a) Push-pull training protocol. The white rectangular frame acts as a cue to attract transient attention, to cause the (vertical) grating in the weak eye to be perceived while the (horizontal) grating in the strong eye is suppressed. (b) Push-only training

protocol. The stimulus presentation sequence is the same as that of the push-pull protocol, except that no grating is presented to the strong eye.

Monocular contrast threshold and orientation discrimination tests at the 2 training locations

The monocular sinusoidal grating (35 cd/m^2 , 3 cpd, 1.25° , 500 msec) was either horizontal or vertical for the contrast sensitivity test, and near-vertical or near-horizontal for the orientation discrimination test (contrast=1.5 log units). The fellow eye viewed a homogeneous field. Each test was conducted using the 2AFC method in combination with the QUEST procedure. Each eye/location/orientation was tested separately in different blocks (50 trials/block), both in the pre-training and post-training phases.

For the contrast threshold test, the temporal sequence of the 2AFC stimulus presentation (Figure 3.4a) was: fixation, interval-1 (500 msec), blank (400 msec), interval-2 (500 msec), blank (400 msec), and mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units, 200 msec). The grating was presented at only one interval while the other interval had a blank field. The observer indicated whether the grating was perceived in interval-1 or -2 by key press, and audio feedback was given. Grating contrast was adjusted after each trial (by QUEST) to obtain threshold.

For the orientation discrimination test, the temporal sequence of the 2AFC stimulus presentation (Figure 3.4b) was the same as in the contrast threshold test. This time however, one interval had a grating whose orientation was slightly different from that in

the other interval. The observer indicated whether the grating with more counterclockwise orientation was perceived in interval-1 or -2 by key press, and audio feedback was given. Grating orientation was adjusted after each trial (by QUEST) to obtain threshold.

Figure 3.4 The 2AFC stimulus presentation sequence for testing: (a) monocular contrast threshold; (b) monocular orientation discrimination.

Stereo threshold and reaction time tests at the 2 training locations and one untrained location

A $7.5^\circ \times 7.5^\circ$ random-dot stereogram (dot size = 0.0132° , 35 cd/m^2) with 1.25° disc target, and random-dot mask ($7.5^\circ \times 7.5^\circ$, 35 cd/m^2) were used. The display contrast was set at 1.5 log units, but at 1.3 or 1.2 log units for two observers to avoid a ceiling effect. Both stereo threshold and reaction time were measured in the pre-training and post-training phases.

We used the standard 2AFC method in combination with the staircase procedure to measure stereo disparity threshold. Figure 3.5a shows the temporal sequence of stimulus presentation: fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and mask (200 msec). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block ended after 10 reversals (~50-60 trials), with average of the last 8 reversals taken as the threshold.

To measure stereo reaction time, the binocular disparity of the stereo disc was either ± 6 arc min (Figure 3.5b). The observer pressed a key immediately upon detecting the stereo disc (1=front, 2=back), and the stimulus was removed. A blank screen (400 msec), followed by a mask (200 msec), ended the trial, and audio feedback was given. If depth was not detected, the stimulus timed-out after 2500 msec. Three 60-trial blocks were tested. The average reaction times of the front and back trials were taken as the final

results. All reaction times with correct responses were longer than 100 msec. We also found the average response accuracy was above 87%, and was larger for the post-training than pre-training trials. Thus, the shorter reaction times after training cannot be attributed to speed-accuracy tradeoff.

Figure 3.5 Stimuli for stereo tests. (a) The 2AFC stimulus presentation sequence for testing stereo threshold. (b) The stimulus presentation sequence for testing stereo reaction times.

3.4 Results

1) SED is reduced significantly under the push-pull training protocol.

To test our first hypothesis, we applied both protocols on the same observer (with an interleaved procedure), at two different retinal locations with similar magnitudes of SED over a 10-day training phase ($n=7$). To monitor the progress of each training session, we measured balance contrast with the orientation of the test grating being either the same as, or orthogonal to, the orientation of the training grating, before and after each day's training session. Figure 3.6a and 3.6b show the average results with the push-pull and push-only protocols, respectively. The x-axis plots the training session and y-axis the interocular balance contrast, which is the difference between the measured balance contrast and fixed contrast (1.5 log units).

Clearly, with the push-pull protocol (Figures 3.6a), the same interocular balance contrast (open symbols) declines as the training progresses [before: slope=-0.026, $R^2=0.881$, $p<0.001$; after: slope=-0.021, $R^2=0.895$, $p<0.001$], indicating perceptual learning. However, the orthogonal interocular balance contrast (filled symbols) changes little [before: slope= -8.82×10^{-5} , $R^2=0.001$, $p=0.919$; after: slope=0.004, $R^2=0.297$, $p=0.103$], suggesting the learning effect is limited to the trained stimulus orientation and eye. We also measured the balance contrast using the method of constant stimuli before and after the entire training period. From the psychometric functions obtained (Figure 3.7a) we calculated the interocular balance contrast (gray symbols, Figure 3.6a), which

confirms a significant learning effect for the same [$t(6)=4.318, p=0.005$] but not for the orthogonal interocular balance contrast [$t(6)=0.218, p=0.835$].

In contrast, the push-only training (Figures 3.6b) shows no learning effects [same interocular balance contrast: before: slope=0.003, $R^2=0.279, p=0.095$; after: slope=0.001, $R^2=0.028, p=0.646$; orthogonal interocular balance contrast: before: slope=-0.001, $R^2=0.079, p=0.403$; after: slope=0.001, $R^2=0.038, p=0.587$]. The interocular balance contrast obtained by the method of the constant stimuli (Figure 3.7a) also fails to demonstrate any significant training effect (t -test, $p>0.05$).

Furthermore, we calculated SED, i.e., the difference between the same and orthogonal interocular balance contrast values. Figure 3.6c plots the SED obtained before each day's training session. Clearly, the push-pull protocol significantly reduces SED (black squares, slope=-0.026, $R^2=0.850, p<0.001$), while the push-only protocol does not (gray diamonds, slope=0.004, $R^2=0.293, p=0.086$). We obtained similar results (not shown) from the SED measured after each day's training session (push-pull: slope=-0.025, $R^2=0.896, p<0.001$; push-only: slope=-0.001, $R^2=0.012, p=0.761$).

Figure 3.6 Changes of interocular balance contrast and SED with push-pull and push-only training protocols in an interleaved procedure (n=7). (a) The average interocular balance contrast with the push-pull training protocol. The interocular balance contrast obtained, respectively, with grating whose orientation was the same as, or

orthogonal to, the grating used in the training, and measured before and after each day's training. Clearly, the balance contrast reduces with days in training when tested with the same orientation grating. (b) The average interocular balance contrast with the push-only training protocol. Overall, the interocular balance contrast does not change with training. (c) Sensory eye dominance (measured before each day's training session) reduces with the push-pull training but not with the push-only training. Both (a) and (b) also include the average data of three observers who were trained with a sequential procedure (plus and cross symbols; error bars are not shown to reduce clutter). Also see Figure 3.7a & b.

Separately, we trained three other observers with a sequential procedure, which is 10 days of push-pull protocol, followed by another 10 days of push-only protocol. The average interocular balance contrast data obtained with the method of constant stimuli are plotted in Figure 3.6a and 3.6b (plus and cross symbols; also see Figure 3.7b). They show a similar trend as the seven observers' data [push-pull: same, $t(2)=4.052$, $p=0.056$, orthogonal, $t(2)=-3.497$, $p=0.073$; push-only: same, $t(2)=0.895$, $p=0.465$, orthogonal, $t(2)=0.325$, $p=0.776$]. Therefore, with the push-only training protocol only, stimulating the weak eye is not sufficient to reduce interocular imbalance in this experimental setting. Essentially, our experiment with the push-pull training protocol reveals that repeatedly suppressing the stimulus image in the strong eye from perception, as “pull”, is necessary to significantly reduce SED.

Additionally, Figure 3.6a and 3.6b also reveal that the magnitudes of the same interocular balance contrast are larger after, than before, each daily training session in both the push-pull [same: $F(1,6)=92.435$, $p<0.001$; orthogonal: $F(1,6)=3.617$, $p=0.106$, 2-way ANOVA with repeated measures] and push-only [same: $F(1,6)=46.802$, $p<0.001$; orthogonal: $F(1,6)=4.464$, $p=0.079$] training protocols. For all conditions, the after/before differences do not vary significantly with the number of training sessions [interaction effect between the after/before and session, $p>0.05$]. The after/before difference in magnitude is significantly larger with the same, than with the orthogonal stimuli, in the push-pull [$F(1,6)=56.935$, $p<0.001$, 2-way ANOVA with repeated measures], as well as in the push-only [$F(1,6)=27.576$, $p=0.002$] training protocols, which is highly suggestive of stimulus orientation and eye specificity. However, this after/before difference is unlikely to be caused by fatigue during the afternoon session, as the measured orientation discrimination data are similar between the morning and afternoon sessions (Figure 3.7c). There is a small but statistically significant learning effect of orientation discrimination [Main effect of the training session, $F(9,54)=2.264$, $p=0.031$; 3-way ANOVA with repeated measures]. However, there is no reliable difference between the orientation discrimination performance in the morning and afternoon [$F(1,6)=1.137$, $p=0.327$]. There is also no reliable difference in performance between the two training protocols [$F(1,6)=2.118$, $p=0.196$]. Furthermore, ANOVA reveals that all interaction effects fail to reach statistical significance ($p>0.05$). Thus, we suggest the after/before difference in interocular balance contrast resembles the observations of performance deterioration

during training in perceptual learning studies of texture discrimination (Mednick et al, 2002; Mednick, Arman, & Boynton, 2005; Ofen, Moran, & Sagi, 2007).

Figure 3.7 Additional data on balance contrast and orientation discrimination thresholds.

(a) & (b) The average balance contrast with the push-pull (left column) and push-only training protocols (right column) obtained using the method of constant stimuli. (a) Data from seven observers trained with the interleaved procedure. (b) Data from three observers trained with the sequential procedure. Overall, with the push-only training (right column), the pre- and post-training psychometric functions for the strong eye overlap, as do those for the weak eye, indicating no change in balance contrast with training. However, for the push-pull training (left column), the weak eye's post-training psychometric function shifts to the left comparing to its pre-training psychometric function, indicating reduced balance contrast after training. Thus, SED is reduced, i.e., learning occurred with the push-pull protocol. (c) The average orientation discrimination threshold decreases as a function of training session for the seven observers trained with the interleaved procedure.

2) Learning effect of SED reduction is retinal location and orientation specific, and maintains even after training stops.

To reveal the underlying learning mechanisms, besides the balance contrast measurements for SED, we conducted three sets of pre- and post-training phase tests on the observers with the interleaved training procedure. Our first set of tests evaluated the hypothesis that the underlying plasticity mainly occurs in the early visual cortex, by investigating the location and orientation specificity of the learning effect (Karni & Sagi,

1991; Schoups, Vogels, & Orban, 1995; Fahle, 1997; Watanabe, Nanez, & Sasaki, 2001). We first measured SED at untrained retinal locations 1.53° from the trained location at the same eccentricity. We found the reduction in SED (0.011 ± 0.033 log units) after the training is much smaller than that at the trained location (0.304 ± 0.043 log units) [$t(6)=6.418, p=0.001$]. Then to verify the orientation specificity of the learning effect, we measured SED at the trained location using a pair of gratings with untrained oblique orientations ($45^\circ/135^\circ$). We also found a very small reduction in SED (0.021 ± 0.048 log units). These findings suggest that the acquired learning in the push-pull protocol is confined to the trained location and orientation.

To evaluate our prediction that the learning effect of SED reduction at the push-pull training location has long maintenance, we measured the SED at three intervals of one-week (W1), two-week (W2), and three-week (W3) after the training ended for the seven observers with interleaved procedure. We found that the average SEDs maintain quite small for all three intervals (W1: 0.202 ± 0.081 ; W2: 0.182 ± 0.068 ; W3: 0.185 ± 0.075 log units), which are similar as the SED at the end of the training (0.159 ± 0.076 log units), while significantly reduced compared to the SED before training (0.463 ± 0.063 log units) [W1: $t(6)=5.393, p=0.002$; W2: $t(6)=5.870, p=0.001$; W3: $t(6)=4.642, p=0.004$]. It further supports that reduced SED is due to the long-term neural plasticity occurring at early visual cortex, rather than a short-term change of cognitive decision making.

3) Small changes of monocular contrast detection and orientation discrimination thresholds can not account for SED reduction.

Our second set of tests addressed the possibility that perceptual learning in the push-pull protocol is accompanied by: (i) reduced efficiency of the strong eye, and/or (ii) increased efficiency of the weak eye (Figure 3.1a). Such modifications in monocular efficiency can be reflected in corresponding changes in monocular contrast detection and orientation discrimination thresholds before and after the training. We thus measured monocular contrast thresholds at the push-pull and push-only training locations using either the grating with the same orientation as, or orthogonal to, the orientation of the weak eye's training grating. Figure 3.8a shows threshold reduction in all conditions, except for that at the push-only location in the strong eye with orthogonal orientation. However, the reduction is much smaller than the reduction in SED at the push-pull location. This suggests that modifications of efficiency within each ocular pathway are unlikely to be the main factor responsible for the learning effect in the push-pull protocol. Similarly, we measured monocular orientation discrimination thresholds, and found a small but statistically insignificant improvement after both training protocols (Figure 3.8b). These findings indicate that alterations of monocular efficiency (factors (i) and (ii) above) are unlikely to have significant contributions to the learning effect of reduced SED.

Figure 3.8 Results on unrelated monocular and binocular functions from the two training protocols. (a) The reduction in monocular contrast threshold at the push-pull (black bars) and push-only (gray bars) training locations, in the weak and strong eye. (b) The

reduction in monocular orientation discrimination threshold. (c) The reduction in stereo threshold for detecting a disc in a random-dot stereogram at the push-pull (black bar), push-only (gray bar), and an untrained (open bar) location. (d) The reduction in reaction time. The asterisks (*) indicate the data whose p values in a t -test are smaller than 0.05.

4) Improvements in stereo abilities are found at the push-pull training location.

Our third set of tests verified the prediction that reducing SED is beneficial for binocular visual processing of stereopsis. We measured binocular disparity threshold and reaction time to detect the depth of a disc in a random-dot stereogram at the trained and untrained locations. We found depth threshold reduces significantly at the push-pull [$t(6)=5.354, p=0.002$] but not the push-only [$t(6)=1.294, p=0.243$] location (Figure 3.8c), with the reduction in the former being significantly larger [$t(6)=2.824, p=0.030$]. Similarly, reaction times to detect depth are reduced significantly at the push-pull [$t(6)=3.104, p=0.021$] but insignificantly at the push-only location [$t(6)=2.086, p=0.082$]. However, the pre and post- reaction time difference does not reveal a statistically significant effect of training protocol [$t(6)=1.600, p=0.161$]. At the untrained locations ($>1.53^\circ$ from the trained location), there are no reliable changes in depth threshold [$t(4)=-1.712, p=0.162$] and reaction time [$t(4)=-0.055, p=0.958$]. Therefore, stereopsis is improved effectively as a consequence of the push-pull protocol which aims at re-balancing interocular inhibition.

3.5 Discussion

In the current experiment, we designed a novel push-pull training protocol, with which an observer's SED is significantly reduced. During each training trial, a square frame acting as an attention cue is presented to the weak eye to cause the dominance of the half-image (vertical grating) viewed by the weak eye (push) and the suppression of the half-image (horizontal grating) viewed by the strong eye (pull). Importantly, this strategy in the push-pull protocol is different from the more conventional "push-only" protocol, where only the weak eye is stimulated (push) with a visual image while the strong eye is not stimulated (no pull). The extra "pull" component presumably reduces the strong eye's transmission efficiency and its effectiveness in suppressing the weak eye (Hebb, 1949), leading to reduced SED and improved stereopsis. Such a learning effect on depth detection is particularly significant, as the training stimuli carried no binocular disparity information and the observers were never trained on the depth detection task during the push-pull training period. It also indicates our novel designed push-pull training protocol is a good candidate treatment for improving binocular visual functions. On the other hand, small changes of monocular contrast detection and orientation discrimination thresholds were found after training, which could not fully account for the SED reduction. Instead, they suggest that the learning effect found with the push-pull protocol is attributable to the activation of interocular inhibition by the weak eye suppressing the strong eye ("pull") during the training trials. In other words, repeatedly

stimulating a putative inhibitory mechanism contributes substantially to adult perceptual learning of the binocular visual system.

Further findings in the current experiment support our hypothesis that the perceptual learning effect on SED with the push-pull training protocol is due to the plasticity of the primary visual cortex (V1). First, we observed that the reduction in SED is limited to the orientation of the stimulus (grating) used during training. No change in SED was found after the training with a test grating orientation that is 45° away from the trained orientation. This indicates that the perceptual learning is orientation specific, which has been considered as a hallmark of early cortical involvement (Karni & Sagi, 1991; Shiu & Pashler, 1992; Schoups, Vogels, & Orban, 1995; Fahle, 1997, 2004). Second, the perceptual learning effect (reduced SED and improved stereopsis) is only found at the trained retinal location, suggesting local neural plasticity. No transfer of the learning at the push-pull location to other locations indicates that the modification of the inhibitory network occurs at cortical areas where the local feature information has not been integrated across a large visual area (Mollon & Danilova, 1996; Xiao et al, 2008; Zhang et al, 2010). These findings are consistent with the response properties of V1 neurons, i.e., orientation selectivity with a narrow tuning function, and relatively small receptive field sizes (McAdams & Maunsell, 1999). Third, the long-lasting learning effect suggests the change does not (only) occur at cognitive level, which usually bears memory deterioration.

Another interesting effect found here is the after/before difference in SED, which is shown with the same stimuli but not with the orthogonal stimuli. This might be due to the contrast adaptation specific to the trained orientation. Since the weak eye is always stimulated by a higher contrast grating than that used in the strong eye during the training, it requires higher balance contrast to reach the neutrality point afterward. Studies with texture discrimination task have revealed similar findings to what we show here that repeated exposure to the visual task leads to performance deterioration within session, which is specific to previously tested retinal locations and stimulus patterns (Mednick et al, 2002; Ofen, Moran, & Sagi, 2004; Mednick, Arman, & Boynton, 2005). These studies have suggested that the deterioration is due to visual adaptation, rather than general fatigue, as specific neural networks in the primary visual cortex become gradually saturated through repeated testing. In the current experiment, it is true that adaptation and perceptual learning both happened with the same stimuli, but not with the orthogonal stimuli, but the occurrence of adaptation is not the necessary condition for learning to happen, as a large after/before difference in balance contrast is also shown with the same stimuli in the push-only training protocol whereas no learning effect is found. Relations between adaptation and perceptual learning have been investigated by studies in visual and multisensory system (Regan & Beverley, 1985; Durgin & Pelah, 1999; Ernst & Banks, 2002; Zwiers et al, 2003). The studies have suggested that a potential mechanism of perceptual learning could be information combination and integration caused by adaptation. Through the adaptation and recalibration, the nervous system plastically

integrates information from different modalities in a statistically optimal way, which is to minimize variance in the final estimate by using maximum-likelihood estimation. Censor, Karni, and Sagi (2006) further investigated the link between perceptual learning, adaptation and sleep. They illustrated that the interaction between consolidation and sleep depends on the adaptation level obtained during the training session. Higher number of training trials induces higher initial discrimination thresholds with a session related to suppressive adaptation processes, but meanwhile facilitates learning. However, the relationship between learning and adaptation is not linear, as overloading training from more trials reduces learning effects. Nevertheless, there are studies demonstrating that perceptual learning is a long-term lasting improvement which has distinct underlying mechanisms from a short-term adaptation (Matthews, Liu, & Qian, 2001; Sur, Schummers, & Dragoi, 2002). The adaptation-induced plasticity, for example in the tilt aftereffect, is caused by a combination of response reduction and broadening of orientation selectivity, together with the shift in orientation (Muller et al, 1999; Dragoi, Sharma, & Sur, 2000; Clifford, 2001). In contrast, the possibly neural basis for pairing-induced plasticity is the altered orientation preference of neurons with increased responses, which results in long-lasting perceptual learning (Schuett, Bonhoeffer, & Hubener, 2001; Yao & Dan, 2001). Our findings might provide some insights on further explorations in adaptation and perceptual learning of interocular imbalance.

Furthermore, our findings indicate potential clinical applications. For patients in post-strabismus surgery, traditional post-surgery amblyopia therapy mainly is solely

patching, which uses a piece of cloth to cover the normal eye, allowing the weak eye to have more opportunities to practice and recover by itself. New treatments applying the perceptual learning paradigm also aim at improving monocular visual ability of amblyopia adult. The drawback of this paradigm of solely stimulating the amblyopic eye (patching the strong eye) is its inefficiency in reducing the inhibition from the strong eye on the amblyopic eye. As it only involves monocular excitatory synapse facilitation, it ignores the balance between the two eyes, which is crucial for binocular functions such as depth perception. Our novel push-pull training protocol is effective due to the cooperative involvement of the inputs from both eyes, and the enhancement of inhibitory synapses strength through anti-Hebbian rules as we hypothesized. This training protocol provides a theoretical but practically feasible approach for the treatment of amblyopia.

3.6 Summary

Perceptual learning in adults is an important means of adapting to the changing environment, and here we designed a novel push-pull training protocol to reduce sensory eye dominance (SED). In the training, an attention cue to the weak eye precedes the stimulation by dichoptic orthogonal gratings. The cue causes the grating in the weak eye to be perceived (push) while the grating in the strong eye is suppressed (pull). We found this push-pull protocol is more effective in reducing SED and improving depth perception than the standard push-only protocol which only trains the weak eye with a monocular grating. The learning effect is retinally localized and orientation specific, suggesting

synaptic modifications in the early visual cortex. We further revealed that the reduced SED is mainly caused by re-balanced interocular inhibition between the strong eye and the weak eye. Our findings suggest that an effective perceptual learning paradigm must address both excitatory and inhibitory networks. Specifically, the substantial role of the inhibitory network found in our study reveals it as a major mediator of cortical plasticity in adult brains. Our study provides the first psychophysical evidence that neural plasticity of an inhibitory network plays a crucial role in adult visual perceptual learning.

CHAPTER 4

EXPERIMENT 3: ROLE OF ATTENTION IN PERCEPTUAL LEARNING

4.1 Rationale

Perceptual learning is a crucial means for the mature perceptual system to maintain agility in a dynamic environment. However, the brain must select what to learn because the early sensory processes are exposed to an overwhelming amount of information. Top-down focal attention, which selects task-relevant stimulus information against competing information, is known to play a critical role in controlling what is learned. Research has shown that, though unconsciously, attention plays an important role in perceptual learning even in tasks involving early visual cortex. Shiu and Pashler (1992) conducted research into improving line orientation discrimination with practice, showing that observers' orientation discrimination did not improve when their attention was focused on brightness (by doing a brightness discrimination task) rather than on the orientation of the lines. They argued that this result suggests that cognitive set affects tuning in orientation channels, perhaps by guiding some form of unsupervised learning mechanism, and that retinotopic feature extraction may not be wholly preattentive. To illustrate the attentional control of early perceptual learning, Ahissar and Hochstein (1993)

tested whether stimulus-specific learning is determined by stimulus-driven mechanisms or high-level attentional mechanisms or both. Using a visual search paradigm, their results showed that practicing one task did not improve performance in another task, even if both of them had the same stimuli but different stimulus attributes to attend. This indicated that specific high-level attentional mechanisms are critical in perceptual learning in that they influence changes at early visual processing levels. Some other studies demonstrated that the effect of learning could be attributed to the enhancement of the spatial attention, guided by visual context or contextual cueing (Chun & Jiang, 1998). Studies on task-irrelevant motion-stimuli (Seitz et al, 2005) have found that learning didn't occur if the motion stimuli were temporally paired within the window of the attentional blink. The mediating function of attention increases as more complex processes are involved in the perceptual learning task (Yotsumoto & Watanabe, 2008).

It is less well known whether the adult brain can selectively learn contextual information presented beyond the focus of top-down attention. If it has this ability, we should be able to reveal a stimulus-driven perceptual learning that is only weakly modulated by top-down attention. In this third experiment, we thus investigated the role of attention in the perceptual learning of reducing sensory eye dominance (SED) by employing a push-pull training protocol which we designed and described in Experiment 2. Our psychophysical finding in the second experiment suggests that the perceptual learning to reduce SED is largely due to early cortical plasticity particularly with respect to the eye-of-origin information. Here, we capitalize on the modulation of interocular

inhibition on eye-of-origin information to reveal perceptual learning beyond the focus of top-down visual attention (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993; Schoups et al, 2001; Watanabe, Nanez, & Sasaki, 2001; Seitz, Kim, & Watanabe, 2009). In our paradigm (Figure 4.1a), two sets of push-pull training stimuli are implemented simultaneously at two different retinal locations with locally large SED (~ 0.3 - 0.4 log units). The observer attends to one set of stimulation and performs an orientation discrimination task, while ignoring the other set. We mainly address two questions: whether top-down attention is necessary for perceptual learning to happen; and, whether top-down attention can facilitate the perceptual learning.

4.2 Hypotheses

We hypothesized that perceptual learning can occur based on a stimulus-driven mechanism in early visual processing beyond the focus of top-down visual attention. Thus, we predicted that a reduction in SED can be found not only at the attended location but also at the unattended location, and that the learning effect is constrained to orientation and eye-of-origin information used in the training.

Second, we predicted that top-down focal attention can facilitate perceptual learning. Our hypothesis is that the facilitation can be expressed at surface representation level with boundary contour (BC) information. In other words, the weak eye's boundary contour signal is expected to be enhanced at the attended location but not the unattended location.

Third, we also hypothesized that the learning effect of reduced SED can be manifested in the dynamics of interocular dominance and suppression, with an advantage at the attended location with the trained stimulus feature.

Finally, we predicted that an improvement of stereopsis ability can be found at both the attended and unattended locations, as SED is decreased at both locations.

4.3 Methods

4.3.1 Design

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 21-inch Samsung SyncMaster flat screen CRT monitor with resolution of 1280 x 1024 at 100 Hz refresh rate (except for BC-based SED test and stereo threshold test: 2048 x 1536 at 75 Hz). Six naïve observers with clinically normal binocular vision and informed consent were tested. We first measured local SED with dichoptic vertical and horizontal grating discs (1.25°) at eight concentric retinal locations 2° from the fovea (0° , 45° , 90° , 135° , 180° , 225° , 270° , and 315°). Two locations with the largest SED were chosen for the training, one for the attended condition and the other for the unattended condition (the two locations had 4° spatial separation for four observers and 2.8° separation for two observers). During the 10-day push-pull training phase, two pairs of orthogonal grating discs (vertical/horizontal) simultaneously stimulated these two retinal locations (Figure 4.1a). While both retinal locations received the same sequence of stimulation (cue, stimulus-1, cue, stimulus-2, mask), the observers

were instructed to only attend to one of the two retinal locations. They were to discriminate the grating orientation of the stimuli at the attended location (vertical vs. near-vertical), and ignore the stimulation at the unattended location. SED at the two training locations were measured before each day's training session to monitor the learning progress. To further assess the learning effect, we made the following measurements at the two training locations in the pre- and post-training phases: (a) boundary contour (BC)-based SED; (b) dynamics of interocular dominance and suppression; (c) stereo threshold; (d) monocular contrast thresholds.

4.3.2 Observers

All six adult observers (ages 27-35) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 40 arc sec), and passed the Keystone vision-screening test. During the experiments they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

4.3.3 Stimuli and procedure

Interocular imbalance test to measure SED at 8 different retinal locations

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m²) (Figure 4.1b). The contrast of the horizontal grating was fixed (1.5 log units) while the contrast of the vertical grating was varied (0-1.99 log units).

A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m²), followed by the presentation of the dichoptic orthogonal grating discs (500 msec), and terminated with a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m², 1.5 log units contrast). The observer responded to his/her percept, vertical or horizontal, by key presses. If a mixture of vertical and horizontal orientation was seen, the observer would respond to the predominant orientation seen. The vertical grating contrast was adjusted after each trial using the QUEST procedure (50 trials/block) until the observer obtained equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. Each block was repeated twice. When the vertical grating was presented to the LE we refer to its contrast at neutrality as the LE's balance contrast. The grating discs were then switched between the eyes to obtain the RE's balance contrast. The difference between the LE and RE balance contrast is defined as the SED.

In the pre-training phase, SED was measured separately at eight concentric retinal locations (0° , 45° , 90° , 135° , 180° , 225° , 270° , and 315°) 2° from the fovea. Thus, a total of 16 stimulus combinations (8 locations x 2 eyes), in a randomized testing order, were run. From the eight retinal locations tested, two locations with the largest SED (~ 0.3 - 0.4 log units) were chosen for the training. During the training-phase, the SED at the two training-locations were measured with horizontal and vertical gratings before each day's training session.

Push-pull training protocol at the attended and unattended retinal locations

The two retinal locations chosen for training were randomly assigned to the attended and unattended conditions, which were implemented simultaneously (Figure 4.1a). A trial began with fixation at the nonius target. Then, at each retinal location, a transient attention cue ($1.25^\circ \times 1.25^\circ$ frame with dash outline, width= 0.1° , 1.52 log units, 70 cd/m^2) was presented monocularly to the weak eye for 100 msec (Ooi and He, 1999). After a 100 msec cue-lead-time, a pair of dichoptic horizontal and vertical gratings (500 msec, 1.25° , 3cpd, 35 cd/m^2) was presented. The same 100 msec cue was presented again 400 msec later, followed by a 100 msec cue-lead-time, and the presentation of a second pair of dichoptic gratings (500 msec). The grating orientation shown to the weak eye in this second presentation had a slightly different orientation from the grating shown in the first presentation. Four hundred msec after the dichoptic grating presentation a binocular checkerboard sinusoidal grating mask (200 msec, $7.5^\circ \times 7.5^\circ$, 3 cpd, 35 cd/m^2 , 1.5 log units contrast) terminated the trial. The contrast values of the dichoptic gratings were those that led to the points of neutrality in the RE and LE with the interocular imbalance test. During the trial, the observer was instructed to attend only to one retinal location (attended condition) and ignore the stimulation at the other retinal location (unattended condition).

Before commencing the proper training phase, we determined for each observer that the cue successfully suppressed the grating viewed by the strong eye. For the stimulation at the attended location, the observer reported by key press whether the first or second interval's grating had a slight counterclockwise orientation, and audio feedback was

given. Fifty such trials were run for each experimental block in order to obtain the orientation discrimination threshold using the QUEST procedure. Twelve blocks were performed during each training day.

Figure 4.1 Stimuli for Experiment 3. (a) For the training, two retinal locations, one for the attended condition and the other for the unattended condition, are simultaneously stimulated. At each location, a white rectangular frame acts as a cue to attract transient attention, causing the (vertical and near-vertical) gratings in the weak eye to be perceived while the (horizontal) gratings in the strong eye are suppressed. The observer performs an orientation discrimination task of the gratings seen by the weak eye at the attended location. (b) Horizontal and vertical gratings are used to measure the contrast SED and interocular dynamics. (c) Stimulus for boundary contour-based SED comprises a pair of dichoptic vertical and horizontal grating discs with vertical grating surrounding. The spatial phase of the vertical grating disc relative to the vertical surround is shifted to obtain the point of neutrality. (d) Similar to (c) except that the gratings are oriented 45° and 135° and the point of neutrality is obtained from the relative phase shift of the 135° grating disc. (e) Random-dot stereogram stimulus is used to measure binocular disparity threshold for seeing a disc target in depth.

Boundary contour (BC)-based SED

We adapted a stimulus from Xu et al (2010) to reveal the contribution of the boundary contour to SED. The stimulus comprised a pair of dichoptic vertical (1.8 log units contrast) and horizontal (1.2 log units contrast) sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2), each surrounded by vertical grating (3 cpd, $7.5^\circ \times 7.5^\circ$, 1.8 log units, 35 cd/m^2) (Figure 4.1c). The disc with the vertical grating in one half-image had a variable

phase-shift (0-180 degrees) relative to the larger vertical grating surround. A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) and the presentation of the dichoptic stimulus (500 msec), followed by a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.8 log units). The observer responded to his/her percept, vertical or horizontal, by key presses. If a mixture of vertical and horizontal orientation was seen, the observer would respond to the predominant orientation seen. The relative phase-shift of the vertical grating disc was adjusted after each trial (step size = 14 degree phase-shift) until the observer obtained an equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. This was done using the staircase procedure. Each block of trials (~50-60 trials) comprised 30 reversals, and the last 26 reversals were taken as the average threshold. When the vertical grating disc was presented to the LE we refer to its phase-shift at the point of neutrality as the LE's balance phase-shift. The grating half-images were then switched between the eyes to obtain the RE's balance phase-shift. The difference in the balance phase-shift between the LE and RE is defined as the BC-based SED. We tested 4 stimulus combinations [2 locations (attended + unattended) x 2 eyes]. Each combination was repeated twice. The order of testing was randomized.

Separately, the BC-based SED was also tested using 45° (1.2 log units contrast) and 135° (1.8 log units contrast) grating discs (1.25° , 3 cpd, 35 cd/m^2 , 500 msec), each surrounded by 135° grating (3 cpd, $7.5^\circ \times 7.5^\circ$, 1.8 log units contrast, 35 cd/m^2) (Figure 4.1d). The staircase method was used, and the relative phase-shift of the 135° grating disc

relative to the 135° surround grating was adjusted after each trial (step size=14 degree phase-shift) until the point of neutrality was obtained for each eye.

Dynamics of interocular dominance and suppression

The stimulus comprised a pair of dichoptic vertical and horizontal grating discs (1.25°, 3 cpd, 35 cd/m², 1.5 log units contrast) surrounded by a 7.5°x7.5° gray square (35 cd/m²) (similar to Figure 4.1b). A trial began with central fixation on the nonius target (0.45°x0.45°, line width=0.1°, 70 cd/m²) and the presentation of the dichoptic orthogonal gratings (30 sec), followed by a 1 sec mask (7.5°x7.5° checkerboard sinusoidal grating, 3 cpd, 35 cd/m², 1.5 log units contrast). The observer's task was to report (track) his/her instantaneous percept of the binocular competitive stimulus over the 30 sec stimulus presentation duration. Depending on the percept, vertical, horizontal, or a mixture of both, he/she would depress the appropriate key until the next percept took over. The predominance (sum of dominance duration/ total tracking duration), average duration (sum of dominance duration/ dominance times) and frequency (dominance times/ total tracking duration) of seeing each percept were calculated.

Two grating orientation conditions were conducted: “same grating” vs. “orthogonal grating”. The same grating condition had the stimulus grating orientation presented to each eye being the same as the trained grating orientation. The orthogonal grating condition had the grating orientation switched between the two eyes. Altogether, there

were 4 stimulus combinations [2 locations (attended + unattended) x 2 conditions (same + orthogonal)]. Each combination was repeated 10 times, with its order randomized.

Stereo threshold

A $7.5^\circ \times 7.5^\circ$ random-dot stereogram (dot size = 0.0132° , 35 cd/m^2) with a variable crossed-disparity disc target (1.25°) was used (Figure 4.1e). The contrast of the stereogram was individually selected for each observer, to make the stereo task moderately difficult and to avoid a possible ceiling-effect due to pixel-size constraint. With this criterion, the contrast levels were set at 1.1 log units for one observer, 1.2 log units for 3 observers, and 1.3 and 1.5 log units, respectively, for the remaining two observers.

We used the standard 2AFC method in combination with the staircase procedure to measure stereo disparity threshold. The temporal sequence of stimulus presentation was fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and random-dot mask (200 msec, $7.5^\circ \times 7.5^\circ$, 35 cd/m^2). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~50-60 trials), and the average of the last 8 reversals were taken as the threshold. Each block was repeated 4 times, and measured over two days. The order of testing was “ABBA” for day-1 and “BAAB” for day-2 (“A” = attended condition and “B” = unattended condition).

Monocular contrast threshold

The monocular sinusoidal grating (1.25° , 3 cpd, 35 cd/m^2 , 500 msec) was either horizontal or vertical for the contrast sensitivity test. The fellow eye viewed a homogeneous field. The test was conducted using a 2AFC method in combination with the QUEST procedure. The 2AFC stimulus presentation sequence was: fixation, interval-1 (500 msec), blank (400 msec), interval-2 (500 msec), blank (400 msec), and mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units contrast, 200 msec). The grating was presented at only one interval while the other interval had a blank field. The observer responded to seeing the grating either in interval-1 or -2 by key press, and audio feedback was given. The grating contrast was adjusted after each trial (by QUEST) to obtain the threshold. We tested 8 stimulus combinations [2 locations (attended+unattended) $\times$ 2 conditions (same + orthogonal) $\times$ 2 eyes] in a randomized order. Each stimulus combination was repeated over 2 blocks of trials (50 trials/block).

4.4 Results

1) SEDs are reduced at both the attended and unattended locations with the trained stimulus feature.

We measured the balance contrast before each day's training session to monitor the progress of perceptual learning at the attended and unattended training locations. At each location, the balance contrast was tested with dichoptic gratings whose orientation in each eye was either the same as, or orthogonal to, the orientation of the grating used

during the training. To be succinct, we shall call the former stimulation the “same grating” and the latter the “orthogonal grating”.

Figures 4.2a and 4.2b plot the interocular balance contrast that is defined as the difference between the measured balance contrast and 1.5 log units (contrast of the fixed grating). With the same grating, we found the mean interocular balance contrast at the attended location (open squares, Figure 4.2a) declines toward the balance point (horizontal dashed line) as the training progresses [slope=-0.0232, $R^2=0.8683$, $p<0.001$]. In contrast, with the orthogonal grating at the attended location, the mean interocular balance contrast (filled squares, Figure 4.2a) only tends slightly toward the balance point [slope=0.0068, $R^2=0.7749$, $p<0.001$] with a much flatter slope [the interaction effect of 2-orientation vs. 11-training session: $F(10, 50)=9.742$, $p<0.001$, 2-way ANOVA with repeated measures]. This finding reinforces those found in our second experiment that the learning effect with the push-pull protocol is orientation and eye specific.

Interestingly, we found a similar learning effect at the unattended location. The mean interocular balance contrast with the same grating (open diamonds, Figure 4.2b) reduces toward the balance point as the training progresses (slope=-0.0146, $R^2=0.8544$, $p<0.001$). However, the mean interocular balance contrast with the orthogonal grating (filled diamonds, Figure 4.2b) only shows a weak tendency toward the balance point (slope=0.0016, $R^2=0.133$, $p=0.270$) [interaction effect of 2-orientation vs. 11-training session: $F(10, 50)=3.553$, $p=0.001$, 2-way ANOVA with repeated measures].

We then derived the SED, i.e., the difference between the same grating and orthogonal grating interocular balance contrast values and plotted the data in Figure 4.2c. Clearly, SED reduces gradually with the number of training sessions at both the attended (slope=-0.0300, $R^2=0.8968$, $p<0.001$) and unattended retinal locations (slope=-0.0162, $R^2=0.8136$, $p<0.001$). A comparison between the slopes of the two conditions reveals the slope of the attended condition is significantly steeper than the slope of the unattended condition [$F(10, 50)=3.961$, $p=0.001$, 2-way ANOVA with repeated measures]. Altogether, these results reveal SED is significantly reduced at the unattended training location beyond the focus of top-down attention. However, top-down focal attention can facilitate perceptual learning as evidenced by the finding at the attended condition (Ahissar & Hochstein, 1993; Crist et al, 1997). Additionally, we found that observers' mean threshold of orientation discrimination at the attended location (Figure 4.2d) decreases gradually along the training session [$F(9, 45)=13.097$, $p<0.001$, 1-way ANOVA with repeated measures] and is reduced significantly comparing to the value before training phase [$t(5)=3.961$, $p=0.011$].

Figure 4.2 Results of the push-pull training at the attended and unattended retinal locations. (a) The average interocular balance contrast at the attended location obtained, respectively, with grating whose orientation was the same as, or orthogonal to, the grating used in the training. The same interocular balance contrast is the measured contrast in the weak eye minus 1.5 log units (fixed contrast of grating in the strong eye); whereas the orthogonal interocular balance contrast is the measured contrast in the strong eye minus 1.5 log units (fixed contrast of grating in the weak eye). The same interocular balance contrast reduces significantly with days in training. (b) The interocular average balance contrast at the unattended location exhibits a similar trend as that at the attended location. (c) SED, defined as the difference between the same and orthogonal interocular balance contrast, reduces significant at both the attended and unattended locations as the training

progresses. (d) The average orientation discrimination threshold decreases as a function of training session at the attended location.

2) Boundary contour (BC)-based SED is only reduced at the attended location.

The grating disc stimuli in Figure 4.1b have similar boundary contour (BC) strength (saliency of the circular disc outline enclosing the grating texture) in each half-image. Thus, the SED obtained from changing the relative grating contrast between the RE and LE mainly reflects the feature-based property of SED. We now investigated whether the reduction in SED is associated with a change in the processing of the *boundary contour* information, which can also affect SED (interocular imbalance) (Ooi & He, 2006; van Bogaert, Ooi, & He, 2008; Su, He, & Ooi, 2009, 2010; Xu, He, & Ooi, 2010). We used a BC-based SED test (Figure 4.1c), where the BC strength of the vertical grating disc is varied by changing the relative phase-shift between the vertical grating disc and the surrounding vertical grating. Meanwhile, the relative contrast of the dichoptic gratings remains constant. Doing so allows us to obtain the balance phase-shift, i.e., the point of neutrality between the two eyes. We measured the balance phase-shifts before and after the 10-day training period. If the weak eye strengthens after the training, the phase-shift required to reach the point of neutrality should be smaller than before the training, leading to a reduction in BC-based SED.

Figure 4.3 plots the BC-based SED before and after training. A larger angular reduction in phase-shift indicates a larger reduction in BC-based SED. As shown in

Figure 4.3a, the BC-based SED is significantly reduced at the attended retinal location after the training [$t(5)=2.571, p=0.050$], while it decreases little at the unattended retinal location [$t(5)=0.722, p=0.503$]. Comparison between the two training locations reveals that the reduction in the mean BC-based SED at the attended location is significantly larger [$t(5)=3.332, p=0.021$]. This result suggests that top-down focal attention plays a larger role in perceptual learning of the BC-based mechanism involved in SED.

We also tested a control condition wherein the dichoptic test stimuli comprised 45° and 135° oriented gratings (Figure 4.1d). If the learning effect found for stimuli in Figure 4.1c is contributed by an enhanced BC strength in the weak eye (besides enhanced interior surface feature), we would expect to find a similar learning effect with test stimuli whose grating orientations are different from the trained orientations. Confirming this, the result in Figure 4.3b shows a significant reduction of the BC-based SED at the attended location [$t(5)=2.601, p=0.048$] but an insignificant reduction at the unattended location [$t(5)=1.398, p=0.221$]. Comparison between the two training locations, however, does not reveal a significant difference of the reduction in BC-based SED [$t(5)=0.289, p=0.784$]. This finding of a learning effect only at the attended training location may be attributed to the fact that the BC-based SED is partially mediated by the border ownership selective neurons in the extrastriate cortices (V2 and beyond), which receive robust top-down attention modulation (Zhou, Friedman, & von der Heydt 2000; Qiu, Sugihara, & von der Heydt, 2007).

Figure 4.3 Result of boundary contour-based SED. (a) With the stimuli of horizontal/vertical (Figure 4.1c), the BC-based SED is significantly reduced after the training at the attended location but not at the unattended location. (b) Similar trend is found with the stimuli of 45°/135° (Figure 4.1d).

3) *Learning effect is also expressed in the dynamics of interocular dominance and suppression with an advantage at the attended location with the trained stimulus feature.*

So far, the measured SEDs are based on a detection task with brief stimulus duration (500 msec). Accordingly, the observed training effect largely reflects the early phase of perceptual dominance mediated by the interocular inhibitory mechanism. To reveal how training influences the maintenance of perceptual dominance and its switching frequency (dynamics), we instructed observers to track their perceptual dominance while viewing the binocular competitive stimulus over an extended duration (30 sec). We used dichoptic orthogonal grating stimuli similar to those in Figure 4.1b. The grating orientation stimulating the weak (trained) eye was either the same as, or orthogonal to, that during

the training. From the observers' tracking data, we calculated the predominance, dominance duration and frequency of dominance. The graphs in the left and right panels of Figure 4.4, respectively, for the attended and unattended conditions, present the data as the mean ratios of the performance of the weak eye to that of the strong eye. Thus, a ratio of unity indicates the two eyes performed equally, while a ratio of greater than unity indicates the weak eye performed better for the given stimulus. Figure 4.4a shows that for each condition, the predominance ratio with the same grating stimulus is increased after the training, but does not change much with the orthogonal grating stimulus [$F(1,5)=10.991$, $p=0.021$, 3-way ANOVA with repeated measures]. This reinforces our earlier finding that the learning is specific to the stimulus orientation and eye-of-origin. Comparison between the performance with the same grating stimulus reveals a larger increase of predominance ratio in the attended condition than in the unattended condition [Main effect of training: $F(1,5)=7.295$, $p=0.043$; interaction effect: $F(1,5)=6.814$, $p=0.048$, 2-way ANOVA with repeated measures]. Further analysis reveals a significant increase in predominance ratio at the attended location [$t(5)=2.786$, $p=0.039$] and a moderate increase at the unattended location [$t(5)=2.444$, $p=0.058$]. But for the orthogonal grating stimulus, 2-way ANOVA fails to reveal a reliable impact of the training on the predominance ratio ($p>0.05$).

The mean dominance duration ratios in Figure 4.4b exhibit a similar trend as the predominance ratios in Figure 4.4a. With the same grating stimulus, the dominance duration ratio (weak eye/strong eye) increases after the training, with the larger increase

found at the attended location [Main effect of training: $F(1,5)=7.027$, $p=0.045$; interaction effect between training location and session: $F(1,5)=5.307$, $p=0.069$, 2-way ANOVA with repeated measures]. Further analysis reveals a significant increase in the duration ratio at the attended location [$t(5)=2.741$, $p=0.041$], and a moderate increase in the ratio at the unattended location [$t(5)=2.345$, $p=0.066$] with training. With the orthogonal grating stimulus, the duration ratios do not change reliably with training ($p>0.05$). Notably, the tracking predominance and duration findings here mirror those found with the interocular imbalance test for SED using a detection task. In other words, the same (weak) eye gains the advantage in both the tracking and detection tasks.

The average dominance frequency ratios in Figure 4.4c do not show any learning effect. A 3-way ANOVA with repeated measures analysis reveals no reliable change in the dominance frequency ratio after the training ($p>0.05$).

Figure 4.4 Dynamics of interocular dominance and suppression before (pre) and after (post) the training, measured with gratings whose orientations were either the same as, or orthogonal to, the training gratings. The data are plotted as a ratio of the performance of the weak eye to the strong eye. Thus, a ratio of greater than unity indicates a superior performance in the weak eye for that stimulus. (a) The predominance ratios are significantly increased with the same grating after the training at both the attended and unattended locations, indicating an improvement of the weak eye. (b) The trend of the

dominance duration ratios is similar to (a). (c) The dominance frequency ratios do not change significantly with training.

4) *Perceptual training improves stereo acuity at both the attended and unattended locations.*

We measured binocular disparity thresholds in the pre- and post-training sessions, using a random dot stereogram (Figure 4.1e, an untrained stimulus) at the attended and unattended training locations. As shown in Figure 4.5a, similar reduction in stereo threshold is found at both locations with training [Main effect of the training: $F(1,5)=23.656$, $p=0.005$; interaction effect: $F(1,5)=0.010$, $p=0.926$, 2-way ANOVA with repeated measures].

Figure 4.5 (a) Perceptual learning transfers to another binocular function (stereopsis) with a different task. Binocular disparity thresholds are significantly reduced at both the attended and unattended locations after the training. (b) Monocular contrast thresholds are significantly reduced after the training at the attended and unattended locations in both the weak and strong eyes. However, these generalized and small reductions are unlikely to be associated with the reduction in SED.

5) Small and generalized reduction in monocular contrast thresholds is unlikely associated with changes in SED.

We measured monocular contrast thresholds in the pre- and post-training sessions with horizontal and vertical gratings. Small, but significant reduction in monocular contrast detection thresholds are found after the training at both locations, regardless of eye and stimulus (Figure 4.5b) [Main effect of the training: $F(1,23)=12.005$, $p=0.002$; interaction effect: $F(1,23)=1.609$, $p=0.217$, 2-way ANOVA with repeated measures]. However, this generalized learning effect in monocular contrast threshold is unlikely to be associated with the reduction in SED, and is consistent with our earlier finding in Experiment 2. For example, had the reduction in monocular contrast thresholds been associated with SED reduction, the contrast threshold reduction in the weak eye would be larger than the contrast threshold reduction in the strong eye.

4.5 Discussion

By implementing the push-pull training at the attended and unattended training locations simultaneously, we found a significant reduction of SED and modifications of other visual functions occurring at both locations. The finding at the unattended location thus reveals a stimulus-driven mechanism for perceptual learning beyond the focus of visual attention, although top-down attention facilitates perceptual learning. Monocular cueing during the push-pull training protocol attracts transient, bottom-up attention to the weak eye leading to a perceptual dominance of the weak eye with a suppression of the strong eye (Ooi & He, 1999). The repeated suppression of the strong eye's signals by the weak eye during the training very likely enhances the synaptic efficiency of the weak eye's inhibitory connection which imposes on the strong eye. Meanwhile, the failure of the strong eye to suppress the weak eye could reduce the synaptic efficiency of the strong eye's inhibitory connection which imposes on the weak eye (Hebb, 1949; Stent, 1973; Dan & Poo, 2004). Thus, our current experiment mainly suggests that the plasticity of the interocular inhibitory network, involving modification of eye-of-origin signals, is largely stimulus-driven and less influenced by top-down attention. It is almost impossible for us to choose to focus attention on only one eye or the other, as we have no conscious access to the eye-of-origin information that is explicitly coded by the monocular neurons in the primary visual cortex.

We also show that the participation of top-down attention in perceptual learning facilitates the stimulus-driven learning mechanism. Studies have revealed that focal

attention is critical for perceptual learning (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993; Crist, Li, & Gilbert, 2001; Schoups et al, 2001; Li, Piëch, & Gilbert, 2004; Mukai et al, 2007). For example, an observer only improves in sensitivity to the attended feature after training, but not on other irrelevant features that are ignored during the perceptual task (Shiu & Pashler, 1992). Furthermore, top-down visual attention tends to directly influence the cortical circuitry that represents global surface and figure for signal enhancement and selection (Duncan, 1984; He & Nakayama, 1995; Reynolds & Chelazzi, 2004; Qiu, Sugihara, & von der Heydt, 2007). It is thus more ready to get engaged in the perceptual learning of mid- and high-level visual processes (Ahissar & Hochstein, 1993). In contrast, top-down attention only exerts an indirect and relatively modest effect on early-level visual processes (e.g., V1), presumably through a feedback network from the extrastriate cortices (Kastner & Ungerleider, 2000; Yoshor et al, 2007). Consistent with this analysis, the facilitated learning effect found at the attended location is revealed more explicitly with a SED test based on the strength of a boundary contour, which is associated with surface processing (Ooi & He, 2006; van Bogaert, Ooi, & He, 2008; Su, He, & Ooi, 2009, 2010; Xu, He, & Ooi, 2010). This also gives us some insight to disassociate two potential mechanisms, grating feature and boundary contour, involved in the perceptual learning of interocular inhibition, which brings up the main question we will address in the next chapter.

There is another possible mechanism accounting for the perceptual learning at the unattended training location: a *stimulus-reward pairing learning mechanism* (Dayan &

Balleine, 2002; Seitz et al, 2009; Sasaki, Nanez, & Watanabe, 2010). A series of studies with global motion direction task discovered that observers can improve their performance in detecting features that are irrelevant to the task used in the training phase (Watanabe, Nanez, & Sasaki, 2001; Watanabe et al, 2002; Seitz et al., 2009). Further studies reveal that task-irrelevant perceptual learning (TIPL) occurs only when the task-irrelevant feature is subthreshold and when its presentation coincides with the onset of the task relevant stimulus during training (Tsushima, Seitz, & Watanabe, 2008; Seitz et al, 2009). It has been proposed that during a training trial, a subthreshold task-irrelevant stimulation can be strongly enhanced by paired reward signals; at the same time, it is not subject to attentional suppression (Seitz et al, 2009). Nevertheless, there are studies with other visual tasks (e.g., orientation discrimination) and tactile tasks showing TIPL can also occur for a suprathreshold feature under exposure to or coactivation with the attended stimulus (Pleger et al, 2001; Dinse et al, 2003; Pleger et al, 2003; Gutnisky et al, 2009). Thus, task-irrelevant learning occurs as long as a training condition is so optimized that task-irrelevant feature signals are internally strong (Seitz & Dinse, 2007). The key to learning is to facilitate the stimulus-related activities to exceed the learning threshold, which is influenced by factors such as attention and reinforcement. Accordingly, this stimulus-reward pairing learning mechanism could plausibly contribute to the perceptual learning of SED at the unattended training location. This is because successful performance in orientation discrimination of the dominant grating disc at the attended location might have triggered the reward system, which consequently caused

learning at the unattended location, since the training stimuli were presented simultaneously at both locations. It is important to emphasize that this plasticity is selectively driven by the binocular competitive stimuli employed in the push-pull training protocol, since in the last experiment we showed that little learning occurred with a push-only training protocol where only the weak eye, but not the strong eye, was stimulated. Consistently, we found very small changes in monocular contrast threshold, but significant modifications in other binocular functions (interocular dynamics and stereo acuity) after training.

4.6 Summary

We thus investigated the role of top-down attention in reducing sensory eye dominance (SED) with a perceptual learning task implementing the push-pull protocol at two retinal locations simultaneously. We found that SED was reduced at both locations, though larger at the attended location, along with consequential changes in other visual functions (BC-based SED, interocular dynamics, and stereo acuity). This indicates early perceptual learning can occur beyond the focus of top-down visual attention through a stimulus-driven mechanism alone, although it is facilitated by focused attention.

CHAPTER 5

EXPERIMENT 4: CONTRIBUTION OF BOUNDARY CONTOUR TO PERCEPTUAL LEARNING

5.1 Rationale

Regarding visual processing of rivalrous stimuli, one question is whether surface properties influence rivalry dominance. The visual system relies on both boundary contours and surface features to represent 3-D surfaces, whose underlying mechanism also determines binocular rivalry perception. When a binocular display has corresponding contours with similar strength in both eyes, a decrease in grating contrast reduces the predominance of that stimulus in one eye; but the change of luminance contrast energy has little influence on the rivalry dynamics if this change also causes the balance of boundary contours of the stimulus in each eye (Ooi & He, 2005). The visual system actively seeks binocular corresponding boundaries, and then implements the occlusion constraint to select the rivaling images for dominance (Ooi & He, 2006). Both first-order and second-order boundary contours, defined by various formats such as luminance and phase-shift, can play very important roles in binocular rivalry dynamics.

In a recent study (Xu, He, & Ooi, 2010) we investigated the question quantitatively by analyzing the contribution of second-order boundary contour strength on binocular rivalry. Analyzing the stimulus characteristics of binocular rivalry can reveal its underlying mechanisms. For instance, from the displays of Binocular Boundary Contour (BBC) and Monocular Boundary Contour (MBC), we found that the boundary contour has a competitive advantage for the dominant percept (Figure 5.1a). We thus varied the relative spatial phase of the gratings to produce the second-order contour in one half-image, to investigate how such half-images with varying illusory boundary contour strengths behave in binocular rivalry. We found that, as to overall dynamics, phase shift affects the predominance of both the vertical and horizontal grating disks. Specifically, the predominance, as well as the dominance duration, of the horizontal grating disk increases significantly with the spatial phase, i.e., the strength of the boundary contour of the disk. The frequencies for seeing all the three percepts also increase significantly with the relative spatial phase. These results demonstrate that binocular rivalry dominance can be affected by the strength of second order contours. Thus, in the current experiment, we further investigated the relationship between surface representation constraints and the plasticity of interocular inhibitory mechanisms.

Figure 5.1 Role of boundary contour in binocular rivalry dominance (Xu, He, & Ooi, 2010). (a) The stimuli used for displays of MBC and BBC conditions with different phase-shifts. (b) Average results analyzed for predominance, dominance duration and alternation frequency.

In the previous two experiments, we varied the grating contrast to find the point of neutrality between the two eyes; and the stimuli used have both interior surface features (grating) and a boundary contour, which could both make contributions to the perceptual learning of interocular imbalance. For example in Figure 4.1b, when the contrast of the grating disc in the half-image is varied, both the interior surface feature (i.e., contrast) and the boundary contour (BC) strength (i.e., saliency of the circular disc outline enclosing the grating texture) change accordingly. Thus, the SED obtained from changing the relative grating contrast between the RE and LE mainly reflects the feature-based property of SED. In this experiment we now investigated whether the reduction in SED is associated with a change in the processing of the *boundary contour* information, which can also affect SED (interocular imbalance) (van Bogaert, Ooi, & He, 2008; Su, He, & Ooi, 2009, 2010). We used a BC-based SED test (Figure 5.2), where the relative contrast of the dichoptic gratings remains constant. We then vary the BC strength of the horizontal grating disc by changing the relative phase-shift between the horizontal grating disc and the surrounding horizontal grating, to obtain the balance phase-shift, i.e., the point of neutrality between the two eyes. Doing so allows us to separate the contributions from feature-based and BC-based cues, and to demonstrate the importance of boundary contour in the learning processing of surface perception.

Figure 5.2 Stimuli for measuring BC-based SED, which comprises a pair of dichoptic vertical and horizontal grating discs with horizontal grating surrounding. The spatial phase of the horizontal grating disc relative to the horizontal surround is shifted to obtain the point of neutrality. BC-based SED is defined as the difference between balance phase-shift in the LE (a) and RE (b).

The purpose of this experiment is to explore the role of the boundary contour in the perceptual learning of interocular imbalance. Especially we aim to compare the different learning effects and mechanisms under monocular and binocular boundary contour conditions, in order to demonstrate the importance of boundary contour in the learning processing of surface perception. We thus designed two push-pull training conditions both with a dichoptic orientation discrimination task (Figure 5.4): (a) monocular boundary contour condition (MBC), where the weak eye is dominant due to the monocular boundary contour while strong eye is suppressed during training with only surface feature (grating); and (b) binocular boundary contour condition (BBC), where the strong eye is suppressed by the weak eye during training with both interior surface feature and boundary contour (by 180 degree phase-shift). We measured the balance phase-shifts before and after the 10-day training period under both conditions. If the weak

eye strengthens after the training, the phase-shift required to reach the point of neutrality should be smaller than before the training, leading to a reduction in BC-based SED.

5.2 Hypotheses

Our hypothesis is that both interior surface feature and boundary contour make contributions to the learning processing of interocular inhibition. Since the local grating features of contrast and orientation are the same under the MBC and BBC training conditions (Figure 5.4), the push-pull protocol (to reduce interocular imbalance) should still work for both of these two conditions through a feature-based mechanism. However, we predicted different learning effects and mechanisms in terms of BC-based SED, because there is only weak eye's monocular boundary contour dominance under the MBC condition, whereas there is boundary contour suppression from weak eye to strong eye under the BBC condition. In other words, interocular inhibition from corresponding binocular boundary contours should facilitate the learning effects with the BBC training condition.

Furthermore, we hypothesized that perceptual learning based on binocular boundary contour has a relatively broader orientation tuning function, so that with the BBC condition, the learning effect of reduced BC-based SED should be able to transfer to untrained stimuli with different orientations from the training stimuli. On the other hand, with the MBC condition, the learning effect might transfer to adjacent retinal locations, as the enhanced monocular boundary contour can impact (suppress) a larger area than

that is trained. This is because there is no boundary contour in the suppressed eye to outline the location explicitly. Additionally, we predicted that the learning effect can also be found in dynamics of interocular rivalry and stereo acuity with both conditions.

5.3 Methods

5.3.1 Design

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 21-inch Samsung SyncMaster flat screen CRT monitor with resolution of 2048 x 1536 at 75 Hz refresh rate (except for contrast SED test: 1280 x 1024 at 100 Hz). All observers (one author and six naïve observers giving informed consent) had normal binocular vision. We first measured local boundary contour interocular imbalance, i.e., BC-based SED, with dichoptic vertical and horizontal grating discs (1.25°) surrounded by a horizontal grating background at eight concentric retinal locations 2° from the fovea (0° , 45° , 90° , 135° , 180° , 225° , 270° , and 315°). Two locations with the largest BC-based SED were chosen for the training, one for the Monocular Boundary Contour (MBC) condition and the other for the Binocular Boundary Contour (BBC) condition. To assess the learning effect, we made the following measurements at the two training locations in the pre- and post-training phases: (a) BC-based SED with dichoptic vertical and horizontal grating discs surrounded by a vertical grating background; (b) BC-based SED with dichoptic 45° and 135° grating discs surrounded by a 135° grating background; (c) contrast SED (interocular imbalance) with

dichoptic vertical and horizontal grating discs; (d) dynamics of interocular dominance and suppression with dichoptic vertical and horizontal grating discs surrounded by a horizontal grating background; (e) stereo threshold with random-dot stereogram. During the 10-day Push-Pull training phase, the MBC and BBC conditions were randomly assigned to two retinal locations with the largest SED respectively (Figure 5.4), and implemented on the same day. The observers were to discriminate the grating orientation of the stimuli (stimulus-1, stimulus-2, mask). To monitor the learning progress, BC-based SED at the training locations were measured before and after each day's training session. Additionally, after the training, BC-based SED was measured at locations ($\pm 45^\circ$) adjacent to the two training locations. (Note that only one, instead of two, adjacent location was measured for each trained location if the two trained locations were less than 90° apart. The average data were taken from two adjacent locations.)

5.3.2 Observers

All seven adult observers (ages 22-28) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 40 arc sec), and passed the Keystone vision screening tests. During the experiments they viewed the monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

5.3.3 Stimuli and procedure

Boundary contour interocular imbalance test to measure BC-based SED at 8 different retinal locations

We adapted a stimulus from Xu et al (2010) to reveal the contribution of the boundary contour to SED. The stimulus comprised a pair of dichoptic vertical (contrast=1.2 log units) and horizontal (contrast=1.8 log units) sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2), each surrounded by a $7.5^\circ \times 7.5^\circ$ horizontal grating background (35 cd/m^2 , 3 cpd, 1.8 log units) (Figure 5.2). The horizontal grating of the disc had a variable phase-shift (0-180 degrees) relative to the larger horizontal grating background. A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) and the presentation of the dichoptic stimulus (500 msec), followed by a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.8 log units). The observer responded to his/her percept by key presses. The relative phase-shift of the horizontal grating disc was adjusted after each trial (step size = 14 degree phase-shift) until the observer obtained equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. [Monitor resolution was set to $2048 \times 1536 @ 75\text{Hz}$, which produces 76 pixels per degree, i.e., 76 pixels per 3 cycles; thus, the minimal phase-shift we can get is $180 \times 3 \times 2 / 76 = 14.2$ degrees.] This was done using the staircase procedure. Each block of trials (~50-60 trials) comprised 30 reversals, with the last 26 reversals taken as the average threshold. When the horizontal grating disc was presented to the LE, we refer to its phase-shift at the point of neutrality as the LE's balance phase-shift (Figure 5.2a).

Then the grating half-images were switched between the eyes to obtain the RE's balance phase-shift (Figure 5.2b). The difference in the balance phase-shift between the LE and RE is defined as the BC-based SED.

In the pre-training phase, BC-based SED was measured separately at eight concentric retinal locations (0° , 45° , 90° , 135° , 180° , 225° , 270° , and 315°) 2° from the fovea. Thus, a total of 16 stimulus combinations (8 locations x 2 eyes), in a randomized testing order, were run. From the eight retinal locations tested, two locations with the largest SED were chosen for the training. During the training-phase, the SED at the two training-locations were measured with horizontal/vertical gratings (surrounded by a horizontal grating background) before and after each day's training session. Additionally, the BC-based SED was measured at locations ($\pm 45^\circ$) adjacent to the two training-locations after the training. Separately, BC-based SED at the two training-locations were further tested with:

- (i) the method of constant stimuli procedure. The relative phase-shift of horizontal grating adopted one of seven levels (0, 30, 60...180 degrees). Each trial was repeated 7 times/block over 6 blocks.
- (ii) A pair of dichoptic vertical (contrast=1.8 log units) and horizontal (contrast=1.2 log units) sinusoidal grating discs (3 cpd , 1.25° , 35 cd/m^2), each surrounded by a $7.5^\circ \times 7.5^\circ$ vertical grating background (35 cd/m^2 , 3 cpd , 1.8 log units) (Figure 5.3a). The vertical grating of the disc had a variable phase-shift (0-180 degrees) relative to the larger vertical grating background.
- (iii) A pair of dichoptic 45° ($1.2\text{ log units contrast}$) and 135° ($1.8\text{ log units contrast}$) grating discs (1.25° , 3 cpd , 35 cd/m^2 , 500 msec), each surrounded by a $7.5^\circ \times 7.5^\circ$ 135° grating background (3 cpd , 35 cd/m^2 , 1.8 log

units contrast) (Figure 5.3b). The staircase method was used, and the relative phase-shift of the 135° grating disc relative to the 135° grating background was adjusted after each trial (step size = 14 degree phase-shift) until the point of neutrality was obtained for each eye. These three measures were performed again in the post-training phase.

Figure 5.3 Stimuli for Experiment 4. (a) Stimulus for boundary contour-based SED comprises a pair of dichoptic vertical and horizontal grating discs with vertical grating surround. The spatial phase of the vertical grating disc relative to the vertical surround is shifted to obtain the point of neutrality. (b) Similar to (a) except that the gratings are oriented 45° and 135° and the point of neutrality is obtained from the relative phase shift of the 135° grating disc. (c) Horizontal and vertical gratings are used to measure the contrast SED. (d) Random-dot stereogram stimulus is used to measure binocular disparity threshold for seeing a disc target in depth.

The MBC and BBC training conditions (Push-Pull protocol) at the 2 retinal locations

Two retinal locations with the largest BC-based SED (~ 40 -50 degrees) were chosen for training. These locations were randomly assigned for the MBC and BBC training conditions (Figure 5.4). For the MBC condition, the stimulus comprised a pair of dichoptic vertical (contrast=1.2 log units) and horizontal (contrast=1.8 log units) sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2), each surrounded by a $7.5^\circ \times 7.5^\circ$ vertical grating background (35 cd/m^2 , 3 cpd, 1.2 log units). The vertical grating of the disc had no (0 degree) phase-shift relative to the larger vertical grating background, which lead to a monocular boundary contour only formed by the horizontal grating disc. For the BBC condition, the stimulus was the same as used in the MBC condition except the vertical grating of the disc had a 180 degree phase-shift relative to the larger vertical grating background, which lead binocular boundary contours formed by both horizontal and vertical grating discs.

During the training, a trial began with fixation at the nonius target. Then, at a chosen retinal location, a pair of dichoptic gratings (500 msec) was presented. Four hundred msec later, another pair of dichoptic gratings (500 msec) was presented. The horizontal grating, which was always shown to the weak eye, in this second presentation had a slightly different orientation from the grating shown in the first presentation. Four hundred msec after the dichoptic grating presentation a binocular checkerboard sinusoidal grating mask (200 msec, $7.5^\circ \times 7.5^\circ$, 3 cpd, 35 cd/m^2 , 1.8 log units contrast) terminated the trial. Due to the higher contrast and boundary contour strength of the disc in the weak eye,

the horizontal grating in the weak eye can always successfully suppress the vertical grating viewed by the strong eye. The observer reported by key press whether the first or second grating had the slight counterclockwise orientation, and audio feedback was given. Fifty such trials were run for each experimental block in order to obtain the orientation discrimination threshold using the QUEST procedure. Twelve blocks were performed for each condition during each day of training, which comprised two separate 1-hour sessions. During each session, the sequence of two training conditions was interleaved by ABBA order.

(a) MBC training paradigm

(b) BBC training paradigm

Figure 5.4 Stimuli and presentation sequence for two training conditions. (a) MBC training condition. Higher contrast and BC strength cause the (horizontal) grating in the weak eye to be perceived while the (vertical) grating in the strong eye is suppressed. (b) BBC training condition. The stimulus presentation sequence is the same as that of the

MBC condition, except that the vertical grating disc in the strong eye also has boundary contour produced by the relative phase-shift against the background.

Contrast interocular imbalance test at the 2 training-locations

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2) (Figure 5.3c). The contrast of the vertical grating was fixed (1.5 log units) while the contrast of the horizontal grating was varied (0-1.99 log units). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2), the presentation of the dichoptic orthogonal grating discs (500 msec), and terminated with a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units contrast). The observer responded to his/her percept by key presses (“0”=vertical, “.”=horizontal). The horizontal grating contrast was adjusted after each trial using the QUEST procedure (50 trials/block), until the observer obtained equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. When the horizontal grating was presented to the LE we refer to its contrast at neutrality as the LE’s balance contrast. Then the grating discs were switched between the eyes to obtain the RE’s balance contrast. The difference between the LE and RE balance contrast is defined as the contrast interocular imbalance. We tested 4 stimulus combinations [2 locations (MBC + BBC) x 2 eyes]. Each combination was repeated twice. The order of testing was randomized.

Dynamics of interocular dominance and suppression at the 2 training-locations

The stimulus comprised a pair of dichoptic vertical (contrast=1.2 log units) and horizontal (contrast=1.8 log units) sinusoidal grating discs (3 cpd, 1.25° , 35 cd/m^2), each surrounded by a $7.5^\circ \times 7.5^\circ$ horizontal grating background (35 cd/m^2 , 3 cpd, 1.8 log units) (similar as shown in Figure 5.2). The horizontal grating of the disc had a 72 degrees phase-shift relative to the larger horizontal grating background. A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) and the presentation of the dichoptic orthogonal gratings (30 sec), followed by a 1 sec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.8 log units contrast). The observer's task was to report (track) his/her instantaneous percept of the binocular rivalry stimulus over the entire 30 sec stimulus presentation. Depending on the percept, he/she would press the appropriate key until the next percept took over. The predominance, average duration and frequency of seeing each percept were calculated.

Two grating orientation conditions were conducted: "same grating" vs. "orthogonal grating". The same grating condition had the binocular rivalry grating orientation presented to each eye being the same as the trained orientation. The orthogonal grating condition had the grating orientation switched between the two eyes. Altogether, there were 4 stimulus combinations [2 locations (MBC + BBC) x 2 conditions (same + orthogonal)]. Each combination was repeated 10 times, with its order randomized.

Stereo threshold test at the 2 training-locations

A $7.5^\circ \times 7.5^\circ$ random-dot stereogram (dot size = 0.0132° , 35 cd/m^2) with a variable crossed-disparity disc target (1.25°) was used (Figure 5.3d). The contrast of the stereogram was individually selected for each observer, to make the stereo task moderately hard and to avoid a possible ceiling-effect due to pixel-size constraint. With this criterion, the contrast levels were set at 1.2 log units for one observer, 1.3 log units for three observers, 1.5 log units for one observer, and 1.7 log units for the remaining two observers. We used the standard 2AFC method in combination with the staircase procedure to measure stereo disparity threshold. The temporal sequence of stimulus presentation was: fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and random-dot mask (200 msec, $7.5^\circ \times 7.5^\circ$, 35 cd/m^2). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~50-60 trials), with the last 8 reversals taken as the average threshold. Each block was repeated 4 times, and measured over two days. The order of testing was “ABBA” for day-1 and “BAAB” for day-2 (“A” = MBC condition and “B” = BBC condition).

5.4 Results

1) BC-based SED is reduced under both MBC and BBC training conditions with potentially different mechanisms.

In order to investigate the contribution of boundary contour to perceptual learning in reducing sensory eye dominance, we analyzed the learning effects under both monocular

boundary contour (MBC) and binocular boundary contour (BBC) conditions, and also compared the differences between them. To monitor progress during each training session, we measured balance phase-shift with the orientation of the test disc grating being either the same as or orthogonal to the orientation of the disc grating used for training. Note that the orientations of the background grating used for testing and the background grating used for training are orthogonal to each other. The balance phase-shift was measured using the QUEST procedure before and after each day's training session. The average results for the MBC and BBC training conditions are shown in Figure 5.5a & b. Clearly, under the MBC training condition, the same balance phase-shift declines as the training progresses [before: slope=-3.915, $R^2=0.917$, $p<0.001$; after: slope=-3.188, $R^2=0.943$, $p<0.001$], indicating perceptual learning. In contrast, the orthogonal balance phase-shift only *declines* very slightly [before: slope=-0.153, $R^2=0.136$, $p=0.265$; after: slope=-0.697, $R^2=0.752$, $p=0.001$], with a much flatter slope [the interaction effect same/orthogonal and training session: before: $F(10, 60)=10.903$, $p<0.001$, 2-way ANOVA with repeated measures; after: $F(9, 54)=2.098$, $p=0.046$]. This finding suggests that the learning effect does not transfer to a stimulus with orthogonal orientation to the trained disc orientation. So the enhanced boundary contour by perceptual learning is partially contingent on the grating orientation of the disc it belongs to. Under the BBC condition, very similar learning effect is also found. The average interocular balance phase-shift with the same grating reduces significantly toward the balance point as the training progress [before, slope=-3.193, $R^2=0.863$, $p<0.001$; after,

slope=-3.382, $R^2=0.817$, $p<0.001$]. However, the orthogonal balance phase-shift only changes little [before: slope=0.410, $R^2=0.357$, $p=0.052$; after: slope=0.250, $R^2=0.149$, $p=0.271$] [the interaction effect same/orthogonal and training session: before: $F(10, 60)=9.707$, $p<0.001$, 2-way ANOVA with repeated measures; after: $F(9, 54)=10.114$, $p<0.001$].

Additionally, Figure 5.5a and 5.5b also reveal that the magnitudes of the same interocular balance phase-shift are larger after, than before, each daily training session in both the MBC [$F(1,6)=91.176$, $p<0.001$, 2-way ANOVA with repeated measures] and BBC [$F(1,6)=65.113$, $p<0.001$] training conditions. In contrast, the orthogonal interocular balance phase-shift is similar when measured before or after each daily training session for both MBC [$F(1,6)=3.227$, $p=0.123$, 2-way ANOVA with repeated measures] and BBC [$F(1,6)=0.613$, $p=0.463$] training conditions. For all conditions, the after/before differences do not vary significantly with the number of training sessions [interaction effect between the after/before and session, $p>0.15$]. The after/before difference in magnitude is significantly larger with the same, than with the orthogonal stimuli, in the MBC [$F(1,6)=53.055$, $p<0.001$, 2-way ANOVA with repeated measures], as well as in the BBC [$F(1,6)=27.914$, $p=0.002$] training conditions. These results suggest that the after/before difference in interocular balance phase-shift is also specific to stimulus orientation and eye, which is consistent with what we have found in Experiment 2.

We calculated BC-based SED, i.e., the difference between the same and orthogonal balance phase-shift, and Figure 5.5c plots the data obtained before and after each day's

training session. We found that SED measured before each day's training session gradually reduced with training, both under the MBC (slope=-3.762, $R^2=0.898$, $p<0.001$) and BBC conditions (slope=-3.603, $R^2=0.911$, $p<0.001$). We obtained a similar trend from the SED measured after each day's training session (MBC: slope=-2.490, $R^2=0.899$, $p<0.001$; BBC: slope=-3.631, $R^2=0.835$, $p<0.001$). Interestingly, the learning effect of SED significant reduction is similar under these two conditions, which is different from what we predicted [Main effect of training session: before: $F(10,60)=11.792$, $p<0.001$, after: $F(9,54)=4.562$, $p<0.001$; interaction effect between training condition and session: before: $F(10,60)=1.611$, $p=0.125$, after: $F(9,54)=0.481$, $p=0.881$, 2-way ANOVA with repeated measures]. This indicates both MBC and BBC conditions are sufficient for the learning. Note that no pre-leading attention cue is presented in the training of this experiment; SED is reduced as long as the weak eye is dominant and the strong eye is suppressed. In other words, the push-pull training protocol works for reducing BC-base SED with either monocular boundary contour or binocular boundary contour, though we can not exclude their different influences on other learning aspects at this stage. Furthermore, since a significant learning effect of boundary contour enhancement is found even when the background grating orientations of the testing and training stimuli are orthogonal to each other, it suggests that the orientation specificity of learning effect is more constrained to the disc enclosed by boundary contour. Thus, the border ownership of the disc contour is also manifested in our findings (Zhou, Friedman, & von der Heydt, 2000).

Figure 5.5 Changes of interocular balance phase-shift and SED with MBC and BBC training conditions in an interleaved order. (a) The average interocular balance phase-shift with the MBC training condition. The interocular balance phase-shift obtained, respectively, with grating whose orientation was the same as, or orthogonal to, the grating used in the training, and measured before and after each day's training. Clearly, the balance phase-shift reduces with days in training when tested with the same orientation grating. (b) The average interocular balance phase-shift with the BBC training condition, which has similar trend of changes as in MBC condition. (c) BC-base SED (measured before and after each day's training session) reduces with both MBC and BBC training conditions. All (a) to (c) also include the average data from method of constant stimuli. Also see Figure 5.6.

We also measured the balance phase-shift using the method of constant stimuli procedure immediately before and after the entire 10-day training period. The psychometric functions (Figure 5.6) obtained allow us to calculate the balance phase-shift. We applied probit analysis to calculate the tuning functions' mean, which presents the threshold at 50% point, i.e., balance phase-shift, and the tuning functions' standard deviation (SD), which represents the bandwidth, i.e., the slope of the psychometric function. Under the MBC condition, we found a significant learning effect for the same balance phase-shift [pre: 120.413 ± 4.011 deg, post: 88.487 ± 6.960 deg, $t(6)=4.753$, $p=0.003$] but not for the orthogonal balance phase-shift [pre: 69.690 ± 10.485 deg, post:

75.736±8.557 deg, $t(6)=-1.309$, $p=0.238$]. Also under the BBC condition, similar learning effect was found [same balance phase-shift: pre: 119.102±5.161 deg, post: 83.760±8.567 deg, $t(6)=5.477$, $p=0.002$; orthogonal balance phase-shift: pre: 74.813±3.903 deg, post: 80.946±6.746 deg, $t(6)=-0.967$, $p=0.371$]. SED was significantly reduced under both MBC condition [pre: 50.722±8.457 deg, post: 12.751±10.928 deg, $t(6)=3.887$, $p=0.008$] and BBC condition [pre: 44.289±6.671 deg, post: 2.814±7.211 deg, $t(6)=5.086$, $p=0.002$]. The reduction in SED was similar under these two conditions [Main effect of training condition: $F(1,6)=1.592$, $p=0.254$; main effect of training session: $F(1,6)=22.051$, $p=0.003$; interaction effect between training condition and session: $F(1,6)=0.326$, $p=0.589$, 2-way ANOVA with repeated measures]. These findings confirm what we get from the QUEST procedure.

However, interestingly, we found different changes on the bandwidth (SD) of the balance phase-shift tuning function between these two conditions [Interaction effect between training condition and session: $F(1,6)=16.143$, $p=0.007$; interaction effect between same/orthogonal and session: $F(1,6)=17.047$, $p=0.006$, 3-way ANOVA with repeated measures]. Under the MBC condition, the bandwidth did not change for the same balance phase-shift tuning function [pre: 32.454±3.732 deg, post: 31.992±3.885 deg, $t(6)=0.180$, $p=0.863$] but increased significantly for the orthogonal (in the suppressed strong eye) balance phase-shift tuning function [pre: 18.034±3.759 deg, post: 27.779±5.574 deg, $t(6)=-3.776$, $p=0.009$]. In contrast, under the BBC condition, the bandwidth decreased significantly for the same (in the dominant weak eye) balance

phase-shift tuning function [pre: 38.635 ± 5.188 deg, post: 24.714 ± 3.614 deg, $t(6)=3.088$, $p=0.021$] but did not change for the orthogonal balance phase-shift tuning function [pre: 22.975 ± 5.219 deg, post: 26.697 ± 5.138 deg, $t(6)=-0.848$, $p=0.429$]. These findings indicate that there are potentially distinct learning mechanisms underlying these two training conditions, though the learning effects expressed on balance phase-shift changes are similar. On the one hand, under the MBC condition, the boundary contour in the suppressed strong eye was getting blurrier, suggesting that during training a relative broad area (no boundary contour) in the strong eye is weakened by the suppression from weak eye's monocular boundary contour. On the other hand, under the BBC condition, the boundary contour in the dominant weak eye was getting sharper, suggesting a contribution of interocular inhibition from corresponding binocular boundary contours to plasticity.

(a) Results from S3

(b) Average results

Figure 5.6 (a) The representative results from one observer (S3) and (b) the average results of balance phase-shift with the MBC (left column) and BBC (right column) training conditions obtained using the method of constant stimuli. Overall, with the MBC training condition, the pre- and post-training psychometric functions for the strong eye overlap, indicating no change in orthogonal balance phase-shift with training. However, the weak eye's post-training psychometric function shifts to the left comparing to its pre-training psychometric function, indicating reduced same balance phase-shift after

training. With the BBC training condition, similar results are found as with the MBC condition. Thus, BC-based SED is reduced with both training conditions.

2) The learning effect of reduced BC-based SED is not constrained to the training stimuli under the BBC condition.

We also investigated the learning effect of reducing BC-based SED with vertical and horizontal grating discs surrounded by a vertical grating background (Figure 5.3a). Here, the orientations of the background grating used for testing and the background grating used for training are the same; and the strength of boundary contour is changed by the phase-shift of the vertical grating disc against the vertical grating background. We again measured balance phase-shift with the orientation of the test disc grating being either the same as or orthogonal to the orientation of the disc grating used for training. We predict the same balance phase-shift would *increase* after training, since the vertical grating disc was suppressed in the strong eye during the training session. What we found is consistent with our prediction (Figure 5.7a). Under the MBC condition, we found a significant learning effect (increase) for the same balance phase-shift [$t(6)=-3.045$, $p=0.023$] but not for the orthogonal balance phase-shift [$t(6)=1.083$, $p=0.320$]. Also under the BBC condition, similar learning effect was found [same balance phase-shift: $t(6)=-3.344$, $p=0.016$; orthogonal balance phase-shift: $t(6)=2.097$, $p=0.081$]. BC-based SED was significantly reduced under both MBC condition [$t(6)=3.360$, $p=0.015$] and BBC condition [$t(6)=4.420$, $p=0.004$] (Figure 5.7b). The reduction in SED was similar under

these two conditions [Main effect of training session: $F(1,6)=17.980$, $p=0.005$; interaction effect between training condition and session: $F(1,6)=0.045$, $p=0.840$, 2-way ANOVA with repeated measures]. These findings confirm our first results above (Figure 5.5).

Figure 5.7 Additional results of BC-based SED. (a) & (b) With the stimuli of horizontal/vertical (Figure 5.3a), the BC-based SED is significantly reduced after the training both with the MBC and BBC conditions. (c) & (d) With the stimuli of 45°/135°

(Figure 5.3b), significant reduction of BC-based SED is only found under the BBC training condition but not the MBC condition.

To disassociate the contribution of grating feature and boundary contour to the learning effect, we further measured the BC-based SED with 45° and 135° grating discs surrounded by a 135° grating background (Figure 5.3b). Interestingly, we found different learning effects under these two training conditions (Figure 5.7c). Under the MBC condition, no learning effects were found no matter when the variable phase-shift disc was in the weak eye [$t(6)=1.526, p=0.178$] or in the strong eye [$t(6)=-0.284, p=0.786$]. In contrast, under the BBC condition, we found significant learning effects both when the variable phase-shift disc was in the weak eye [$t(6)=3.143, p=0.020$] and in the strong eye [$t(6)=-5.516, p=0.001$]. The SED was significantly reduced under the BBC condition [$t(6)=4.111, p=0.006$] but not under the MBC condition [$t(6)=1.652, p=0.150$], and the comparison between these two training conditions revealed a significant difference of the reduction in SED [Main effect of training session: $F(1,6)=10.317, p=0.018$; interaction effect between training condition and session: $F(1,6)=22.237, p=0.003$, 2-way ANOVA with repeated measures] (Figure 5.7d). Therefore, we further elucidated that the enhanced boundary contour is not completely orientation contingent on its border-ownership surface (disc), because under the BBC condition the learning effect can transfer to testing gratings with 45° different orientations from training gratings. But this requires binocular boundary contour inhibition since this transfer only happens under the BBC condition, in

which the binocular border-ownership selective neurons in the extrastriate cortices (V2 and beyond) are involved in the plasticity of interocular inhibition. Overall, training enhances BC strength, besides interior surface feature, in the weak eye, so that the learning effect is shown at 45° orientation away when tested with BC-based stimuli.

3) The learning effect of reduced contrast SED is only found with the BBC training condition.

Additionally, we also measured the learning effect on contrast SED with vertical and horizontal grating discs surrounded by a gray background (Figure 5.3c). We again measured balance contrast with the orientation of the test disc grating being either the same as or orthogonal to the orientation of the disc grating used for training. We found balance contrast changed differently under these two training conditions (Figure 5.8a). Under the MBC condition, no changes were found for either the same balance contrast [$t(6)=0.474$, $p=0.652$] or the orthogonal balance contrast [$t(6)=-0.672$, $p=0.527$]. In contrast, under the BBC condition, we found a significant learning effect (reduction) for the same balance contrast [$t(6)=6.357$, $p=0.001$] but not for the orthogonal balance contrast [$t(6)=-0.203$, $p=0.846$]. And the contrast SED was significantly reduced under the BBC condition [$t(6)=3.625$, $p=0.011$] but not under the MBC condition [$t(6)=0.758$, $p=0.477$], and the comparison between these two training conditions revealed a significant difference of the reduction in SED [Interaction effect between training condition and session: $F(1,6)=10.328$, $p=0.018$, 2-way ANOVA with repeated measures]

(Figure 5.8b). Therefore, using the push-pull training protocol with binocular corresponding boundary contours, modification of interocular inhibition can be implemented by both feature-based and BC-based mechanisms. In contrast, the MBC push-pull protocol is likely to take effect mainly through BC-based mechanism.

Figure 5.8 Changes of contrast SED at trained locations. (a) With the stimuli of horizontal/vertical (Figure 5.3c), we found a significant reduction for the same balance contrast under the BBC condition. (b) The contrast SED is significantly reduced after the training with the BBC condition but not MBC condition.

4) *The learning effect of reduced BC-based SED is less constrained in the trained retinal location under the MBC condition than the BBC condition.*

To investigate the location specificity of learning effect, we further measured the BC-based SED at untrained retinal locations 1.53° from the trained location at the same eccentricity. As shown in Figure 5.9a, two adjacent locations were measured if MBC and BBC training locations were far apart. But for five observers, their two largest SED locations, which were chosen for training, were less than 90° apart, so only one adjacent

untrained location was measured for each trained location. For the other two observers, two adjacent locations were measured for each training location, and the average data from these two untrained locations were taken for further analysis. We did not find a significant change of interocular balance phase-shifts at the adjacent untrained locations under either MBC [same: $t(6)=1.986$, $p=0.094$; orthogonal: $t(6)=0.496$, $p=0.637$] or BBC condition [same: $t(6)=0.682$, $p=0.521$; orthogonal: $t(6)=0.673$, $p=0.526$] (Figure 5.9b). However, average BC-based SED of adjacent location is reduced significantly under MBC condition [$t(6)=4.638$, $p=0.004$] but not under BBC condition [$t(6)=-0.228$, $p=0.827$]. And the average reduction of BC-based SED at the adjacent retinal locations is much larger under the MBC condition than the BBC condition [Interaction effect between training condition and session: $F(1,6)=10.514$, $p=0.018$, 2-way ANOVA with repeated measures] (Figure 5.9c). Furthermore, we found that this difference is contributed to the different changes for the same balance phase-shift [$F(1,6)=11.059$, $p=0.016$] but not for the orthogonal balance phase-shift [$F(1,6)=0.909$, $p=0.377$] between the two training conditions. This indicates that the learning effect is less retinotopic under the MBC condition than the BBC condition. We suspect that the affected retinal area is broadened under the MBC training condition since no corresponding boundary contour is presented in the suppressed eye to outline the inhibitory area explicitly. Additionally, note that the pre- average SED at the adjacent locations is much smaller than the SED at the location we chose to train, and this indicates the heterogeneity of local SED as shown in Experiment 1.

Figure 5.9 Changes of BC-based SED at adjacent untrained locations. (a) Illustration of tested adjacent locations, which are 1.53° from the trained location at the same eccentricity. (b) There are no significant changes in interocular balance phase-shift of adjacent untrained locations under either training condition. (c) Average BC-based SED at adjacent untrained locations is reduced larger under the MBC condition than the BBC condition.

5) Learning effect is also expressed on the dynamics of interocular dominance and suppression with an advantage under the MBC condition with the trained stimulus feature.

The consequences of reduced BC-based SED are evident in a binocular rivalry tracking task (Figure 5.2) as changes of the maintenance of perceptual dominance. From the observers' tracking data, we calculated the predominance, dominance duration and frequency of dominance. The graphs in the left and right panels of Figure 5.10, respectively, for the MBC and BBC conditions, present the data as the mean ratios of the performance of the weak eye to that of the strong eye. Thus, a ratio of unity indicates the

two eyes performed equally, while a ratio of greater than unity indicates the weak eye performed better for the given stimulus. Using stimuli with the trained orientation (same condition), binocular rivalry predominance ratio (weak eye to strong eye) increases after training, with the larger increase found under the MBC training conditions [Main effect of training session: $F(1,6)=29.276$, $p=0.002$; interaction effect between training condition and session: $F(1,6)=6.216$, $p=0.047$, 2-way ANOVA with repeated measures]. Further analysis reveals a significant increase in the predominance ratio under both MBC [$t(6)=-4.830$, $p=0.003$] and BBC conditions [$t(6)=-5.315$, $p=0.002$]. No reliable changes occurred with the orthogonal stimuli ($p>0.3$).

The mean dominance duration ratios in the middle panel of Figure 5.10 exhibit a similar trend as the predominance ratios in the upper panel. For the same stimulus condition, the dominance duration ratio (weak eye/strong eye) increases after the training under both MBC and BBC conditions, with similar increase [Main effect of training session: $F(1,6)=20.839$, $p=0.004$; interaction effect between training condition and session: $F(1,6)=0.687$, $p=0.439$, 2-way ANOVA with repeated measures]. Further analysis reveals a significant increase in the ratio under both MBC [$t(6)=-4.634$, $p=0.004$] and BBC conditions [$t(6)=-3.262$, $p=0.017$]. With the orthogonal stimuli, no reliable change was found ($p>0.3$).

Changes in dominance frequency ratios are presented in the lower panel of Figure 5.10. For the same stimulus condition, the dominance frequency ratio (weak eye/strong eye) increases after training, with the larger increase found under the MBC training

conditions [Main effect of training session: $F(1,6)=6.890$, $p=0.039$; interaction effect between training condition and session: $F(1,6)=7.306$, $p=0.035$, 2-way ANOVA with repeated measures]. Further analysis reveals a significant increase in the frequency ratio under the MBC [$t(6)=-3.197$, $p=0.019$] but not the BBC condition [$t(6)=-0.695$, $p=0.513$]. No reliable changes occurred with the orthogonal stimuli ($p>0.25$). Notably, out of our expectation, the tracking predominance and frequency changes here don't completely mirror those found with the interocular imbalance test for SED using a detection task, in that with the tracking task the weak eye gains more advantage with the MBC training condition. Therefore, monocular boundary contour suppression is more effective on modifying the maintenance of perceptual dominance.

Figure 5.10 Dynamics of interocular dominance and suppression before (pre) and after (post) the training, measured with gratings whose orientations were either the same as, or orthogonal to, the training gratings. The data are plotted as a ratio of the performance of the weak eye to the strong eye. Thus, a ratio of greater than unity indicates a superior performance in the weak eye for that stimulus. Upper panel: the predominance ratios are

significantly increased with the same grating after the training under both the MBC and BBC conditions, indicating an improvement of the weak eye. Middle panel: the trend of the dominance duration ratios is similar to the predominance ratios. Lower panel: the dominance frequency ratios do not change significantly with training.

6) *Stereo acuity is improved by perceptual training with both the MBC and BBC conditions.*

Figure 5.11 shows that the consequence of reduced BC-based SED is also evident in the reduction of random dots stereogram disparity threshold under both MBC and BBC training conditions, with similar learning effects [Main effect of the training session: $F(1,6)=98.025$, $p<0.001$; interaction effect between training condition and session: $F(1,6)=1.655$, $p=0.246$, 2-way ANOVA with repeated measures. Further analysis reveals a significant decrease in the disparity threshold under both MBC [$t(6)=9.191$, $p<0.001$] and BBC conditions [$t(6)=9.421$, $p<0.001$].

Figure 5.11 Binocular disparity thresholds are significantly reduced with both the MBC and BBC conditions after the training.

5.5 Discussion

In our current experiment, we designed two push-pull training protocols: MBC and BBC, and found that BC-based SED can be effectively reduced under both training conditions. One important modification in the current design is that there is no pre-leading attention cue presented before the orthogonal grating discs during training. Instead, due to the contrast and boundary disadvantages, the vertical grating in the strong eye is suppressed by the horizontal grating in the weak eye automatically, which can cause a efficient learning effect on SED reduction. Therefore, we are able to rule out an alternative explanation regarding the role of the cue in the original push-pull protocol. It is the suppression of the strong eye that matters in an effective perceptual learning of interocular imbalance, instead of the cue priming effect on the weak eye per se.

With the measurement of BC-based SED, we also found the learning effect of interocular imbalance reduction with testing gratings with 45° different orientations from training gratings. One possible explanation is that the orientation tuning function of surface BC has a relatively broad bandwidth. This finding is different from what we found in Experiment 2, where the learning effect of reducing contrast SED did not transfer to the test stimuli whose grating orientations are 45° different from training stimuli. The difference is very likely due to the testing stimuli, which are mainly

feature-based (varying contrast) in Experiment 2, but BC-based (varying phase-shift) in current experiment, which have broader orientation tuning function. At the same time, the current finding is consistent with what we found in Experiment 3, where BC-based SED was reduced significantly at the attended location with $45^{\circ}/135^{\circ}$ oriented gratings. However, what needs to be pointed out is that this transfer only happens under the BBC training condition (current experiment) with the signal enhancement from top-down visual attention (Experiment 3). Therefore, in order to trigger the plasticity of interocular surface processing, both top-down attention and binocular BC suppression must be engaged (He & Nakayama, 1995; Reynolds & Chelazzi, 2004; Ooi & He, 2006; Qiu, Sugihara, & von der Heydt, 2007; Su, He, & Ooi, 2009).

Furthermore, the current finding that the MBC push-pull protocol can reduce BC-based SED but not the contrast-based SED is consistent with the hypothesis that BC-based SED largely reflects the surface BC mechanism underlying interocular inhibition whereas the contrast-based SED mainly involves both the surface BC and surface feature (grating) mechanisms. In contrast, with the BBC push-pull protocol, both feature-based and BC-based mechanisms can take part in the perceptual learning of interocular imbalance. According to the insignificant reduction of contrast SED under the MBC condition, we propose that inhibition from a binocular boundary contour is necessary for the suppression of an enclosed surface (disc) to occur through feature-based processing. The findings on the contrast-based SED along with the one on BC-based SED (oblique) reveal that the learning effect on reduction of SED is significantly larger under

the BBC training condition than the MBC condition. One explanation is based on the fact that the half-image presented to the strong eye carries a boundary contour in the BBC training stimuli but not in the MBC training stimuli. Under the BBC training condition, repetitive suppression of the boundary contour and its interior grating texture in the strong eye during training may degrade the underlying boundary process that deploys interocular inhibition on the weak eye. Thus, it is more efficient for training when the rivalry stimulus involves binocular BC. However, the average reduction in contrast SED (~ 0.15 log units) found under the BBC condition here is (much) smaller than the average reduction (~ 0.3 log units) found in Experiment 2 & 3. This is possibly due to the different manipulations on the training stimuli: with the background grating used in the current training design, a surface BC mechanism is largely engaged in the learning process, which can only be partially assessed by the contrast-based SED test. Nevertheless, in terms of the improvement on other binocular functions, such as stereo acuity, similar effects are found with feature-based and BC-based training stimuli.

In addition, we noticed that the learning effect on binocular rivalry is relatively larger at the MBC training location (predominance and dominance frequency but not dominance duration) than the BBC training location. This might suggest that monocular boundary contour suppression has a bigger advantage at changing the sustained perceptual dominance, though we are still unclear about the underlying mechanism.

5.6 Summary

To investigate the contribution of boundary contours to perceptual learning of interocular imbalance, we carried out two training conditions, MBC and BBC, with the push-pull protocol. We found that BC-based SED is reduced under both MBC and BBC training conditions by a similar amount, though through different mechanisms. With the BBC condition, the learning effect of reduced BC-based SED can transfer to untrained stimuli with different orientations from the training stimuli, and the feature-based contrast SED is also reduced. However, the learning effect of reduced BC-based SED is less constrained in the trained retinal location under the MBC condition than the BBC condition. And the learning effect is also expressed on the dynamics of interocular dominance and suppression with an advantage under the MBC condition. Perceptual training improves stereo acuity with both conditions.

CHAPTER 6

EXPERIMENT 5: GENERALIZATION OF LEARNING EFFECTS

6.1 Rationale

Stimulus specificity of the learning effect is one characteristic of perceptual learning, which indicates the loci for learning to occur within low-level networks in the perceptual system. Earlier studies on perceptual learning (Fiorentini & Berardi, 1980; Ball & Sekuler, 1982) showed that the learning effect is often stimulus-specific in orientation, spatial frequency and other psychophysics detection and discrimination tasks, which implies that perceptual learning happens in an early visual stage within specific channels. Later studies have reported consistently that learning is usually constrained to the practice stimulus (Karni & Sagi, 1991; Ahissar & Hochstein, 1993). This stimulus-specific learning effect has been used to infer the loci where the plasticity occurs, and has become a trademark in most early perceptual learning studies. For instance, learning in motion discrimination is inferred to happen in the visual area MT (medial temporal cortex), where neurons are selectively tuned to motion directions (Ball & Sekuler, 1982). The perceptual learning of interocular inhibition investigated in Experiment 2-4 has also

shown high feature specificity when stimuli with single frequency and orientation are used during training.

However, there are doubts as to whether the training paradigm is what is restricting learning transfer. Though the learning effect for difficult tasks has high specificity, it can be influenced and modified by easy tasks (Ahissar & Hochstein, 1997). By varying stimulus temporal sequence between training sessions, a “bootstrap effect” is demonstrated that practicing simple tasks could boost the speed of learning similar difficult tasks afterwards. Liu and Vaina (1998) addressed this issue by employing a paradigm of simultaneous learning on motion discrimination with an interleaved stimulus sequence A-A-B, A-A-B, ..., where A and B were two directions. They found that participant’s improvement speed on the direction with less frequent trials got faster, implying that it gained learning transfer from the more frequent direction. Further studies (Liu, 1999; Liu & Weinshall, 2000) explored the mechanisms of generalization in perceptual learning on motion direction by implementing a “rooting” paradigm to build the transfer of learning from a simple task to a difficult one. When the task difficulty was reduced by enlarging the difference between motion directions, learning transferred to new motion directions. Similar findings were reported from perceptual learning in the auditory system that the capacity of plasticity of the auditory space map in adult owls is greater than was previously recognized if using small-increment-step training methods (Linkenhoker & Knudsen, 2002; Parthasarathy, 2002). Accordingly, we can expand the clinical significance of our push-pull protocol, if we are able to generalize the learning

effects of reducing SED (interocular imbalance) to stimuli with different orientations from the trained ones.

Orientation and spatial frequency selectivity of primary visual cortex can be characterized by the channel theory that spatial vision comprises a set of narrowband filters or channels to detect certain ranges of physical stimuli (Wilson, McFarlane, & Phillips, 1983; Watt & Morgan, 1985; Watson & Solomon, 1997). Researchers have measured orientation and spatial frequency bandwidths of contrast sensitivity with both physiological methods for V1 neurons and psychophysical paradigms for human observers, including contrast masking, subthreshold summation, and contrast adaptation. Physiological studies in cats and monkeys have shown that orientation bandwidth, measured as full-width at half-height of the tuning function, is around 45° , with a central peak orientation (Wilson & Sherman, 1976; Parker & Hawken, 1988). These bandwidths get a little narrower as spatial frequency increases. Using a contrast masking technique, Campbell and Kulikowski (1966) first estimated the psychophysical orientation bandwidth to be around 30° , which is consistent with the results obtained by later masking studies (Phillips & Wilson, 1984; Blake & Holopigian, 1985). Orientation bandwidth measured by a contrast adaptation paradigm tends to be around 40° (Movshon & Blakemore, 1973; Snowden, 1992), and similar results were also yielded from subthreshold summation studies (Kulikowski, Abadi, & King-Smith, 1973). Most of these behavioral studies also suggested that orientation bandwidth narrows a bit toward higher spatial frequencies.

As to spatial frequency channels, physiological experiments have demonstrated that the typical frequency bandwidth of visual cortical neurons is around 1.5 octaves (Movshon, Thompson, & Tolhurst, 1978; DeValois, Albrecht, & Thorell, 1982). The tuning function is peaked at a central frequency, so that spatial frequencies at up to ± 0.75 octaves will stimulate the neuron to differing degrees. (Note that an octave is a doubling in frequency.) Psychophysical measurements from masking studies have confirmed that spatial frequency bandwidth is about 1.4 octaves (Stromeyer & Julesz, 1972; Wilson, McFarlane, & Phillips, 1983). With a contrast adaptation technique, the bandwidth was estimated to be around 1.5 octaves (Pantle & Sekuler, 1968; Blakemore & Campbell, 1969), and consistent results were obtained by subthreshold summation tests (Sachs, Nachmias, & Robson, 1971; Kulikowski & King-Smith, 1973; Quick & Reichert 1975). Spatial frequency bandwidths were also found to become narrower along with the increase of spatial frequency. Most of these behavioral studies used test spatial frequencies around 1 to 6 cpd; the gratings tested in our experiment with spatial frequency of 3 or 6 cpd fall within this range. Vertical gratings were used as test stimuli in the majority of studies, and there is little psychophysical evidence showing that spatial frequency bandwidth varies with orientation.

In general, qualitatively similar bandwidths have been found with various experimental paradigms: around 40° in orientation and 1.5 octaves in spatial frequency. These channels are relatively independent spatial mechanisms, whereas they can also be influenced by some factors, such as attention (Carrasco, Penpeci-Talgar, & Eckstein,

2000) and spatial context (Polat & Sagi, 1993; Chen & Tyler, 2008). Research has also shown that suppression in binocular rivalry broadens the orientation tuning function (Ling & Blake, 2009). In Experiment 2, no significant reduction in contrast SED can be found with gratings 45° orientation different from the training stimuli, as the learning effect is presumably constrained within 20° (half bandwidth) of the training stimulus. Physiological studies have showed that both orientation and spatial frequency bandwidths get broader from fovea towards periphery (Wilson & Sherman, 1976); but comparing fovea to 2 degree parafovea, there are insignificant differences. In the current experiment, we trained and tested paired gratings with orthogonal orientations, but we aimed to generalize the learning effects from trained pairs to untrained pairs with different orientations. Therefore, we applied stimuli with multiple orientations within one training block, in order to facilitate, or “boost”, the transfer of the learning effect between orientation channels. Additionally, we measured the extent of learning transfer to the untrained frequency (6 cpd), which is 1 octave higher than training frequency (3 cpd).

To achieve our experiment goal, four pairs of grating discs with orthogonal orientations are included in the training session for an orientation discrimination task on the perceived stimulus from the weak eye. The push-pull training protocol is implemented so that a preceding transient cue is presented to guarantee the trained (weak) eye is dominant all the time over the suppressed (strong) eye. For half of the rivalry stimulus, four grating orientations are 0° , 45° , 90° , and 135° (Figure 6.1a-d respectively). Four interleaved QUEST procedures are carried out in one block for four orientations

respectively with random order. This procedure design not only provides counterbalance between different orientations, but also brings uncertainty to the orientation to be tested in next trial, so that it can facilitate the generalization of learning effects across different orientations channels. In this case, the stimuli (1.5° , 3 cpd) with multiple orientations are more similar as in the natural environment, and are presented to the observers' fovea to be close to the daily vision use. After the training phase, we measured the SED changes of the stimuli with trained orientations as well as the untrained orientations, which are between the ranges of trained orientations. We also tested the specificity of spatial frequency of learning effect.

Figure 6.1 (a) - (d) Stimuli for measuring the SED at observer's fovea on four orientations: 0° , 45° , 90° , and 135° respectively. The orientation referred to the grating disc with variable contrast, and the other half of the rivalry stimulus had an orthogonal grating disc (with fixed contrast).

6.2 Hypotheses

Our main hypothesis is that for the foveal retinal location, our push-pull protocol can also effectively change the synaptic efficacy of interocular inhibition by repeatedly stimulating the weak eye while suppressing the strong eye at the same time. Therefore, the interocular imbalance (SED) in the fovea is expected to decrease significantly through perceptual learning of the underlying inhibitory mechanism. We have demonstrated in Experiments 2-4 that local SED in parafovea can be reduced with push-pull training; however, we can not simply assume this protocol will work out with similar results when the training location is in the fovea. In daily life, the fovea is involved in various visual tasks, e.g., fine spatial discrimination, and potential improvement is thought to be more limited than in parafovea (Saugstadt & Lie, 1964; Frendick & Westheimer, 1983). For tasks with existing fine performance (low threshold), such as motion and orientation discrimination for cardinal orientations in fovea, learning potential is less than that for tasks of oblique orientation and parafovea, because the former has been over-trained in everyday life (Vogels & Orban, 1985; Ball & Sekuler, 1987; Beard, Levi, & Reich, 1995). Influential factors involved in perceptual learning are also different for foveal and parafoveal locations. For instance, performance improvement by practice in fovea can be attributed to fine tuning of the neural mechanisms mediating the task (McKee & Westheimer, 1978; Saarinen & Levi, 1994; Lu & Doshier, 2004), while learning occurring in parafovea is also related to improvement of attentional selection, i.e., learning to direct attention to peripheral targets (Saugstadt & Lie, 1964; Nakayama & Mackeben, 1989;

Beard, Levi, & Reich, 1995). Therefore, by presenting the training stimuli (1.5° , 3 cpd) in fovea, we intend to test our hypothesis that plasticity of the inhibitory network still exists in this fully used retinal location. As we all have experienced, SED is not a skill that we can master or improve through daily vision use. Even with a performance-oriented task, for example, random-dot stereoscopic depth perception, as long as it is seldom trained, performance improvements have been found in both in fovea and periphery (Ramachandran & Braddick, 1973; Fredrick & Westheimer, 1983).

Second, we hypothesized that there is a generic mechanism of plasticity in interocular inhibition, besides the learning process which is stimulus specific (as shown in the last three experiments) due to the limitation of orientation and spatial frequency bandwidth. Therefore, we predicted that the training on multiple orientations within one block can boost the learning effects on each other. Accordingly, the SED should be significantly reduced at all four trained orientations within a period much shorter than that would take if these four orientations be trained separately. Furthermore, we proposed that by including various orientations in the training stimuli, the learning effect of SED reduction can be generalized to new pairs of gratings with orientations 22.5° different from the training pairs, since the learning effect is presumably constrained within the half bandwidth of orientation tuning function ($40^\circ/2$). A partial transfer of training frequency is also predicted as the untrained frequency is 1 octave higher than the training frequency, while learning effect is mostly constrained within 1.5/2 octaves.

6.3 Methods

6.3.1 Design

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 21-inch Samsung SyncMaster flat screen CRT monitor with resolution of 1280 x 1024 at 100 Hz refresh rate (except for stereo threshold test: 2048 x 1536 at 75 Hz). Eight naïve observers with clinically normal binocular vision and informed consent were tested. We first measured the SED with two pairs (vertical/horizontal, and $45^\circ/135^\circ$) of dichoptic grating discs (1.5°) at fovea. During the 10-day Push-Pull training phase, four pairs of orthogonal grating discs stimulated the foveal location with four interleaved QUEST procedures with a random order. For half of the rivalry stimulus, the four grating orientations are 0° , 45° , 90° , and 135° . With a 2AFC sequence of stimulation (cue, stimulus-1, cue, stimulus-2, mask), the observers were instructed to discriminate the grating orientation (e.g., vertical vs. near-vertical). SED was measured before and after each day's training session to monitor the learning progress. To further assess the learning effect, we made the following measurements at fovea in the pre- and post-training phases with the sequence listed as follows: 1) interocular imbalance test to measure SED at fovea of [(a) different contrast levels; (b) untrained orientations; (c) untrained spatial frequency]; 2) dynamics of interocular dominance and suppression; 3) stereo threshold.

6.3.2 Observers

All eight adult observers (ages 23-33) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 40 arc sec), and passed the Keystone vision screening test. During the experiments they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

6.3.3 Stimuli and procedure

Interocular imbalance test to measure SED at fovea

We measured the SED at four orientations: 0° , 45° , 90° , and 135° (Figure 6.1a-d respectively). The orientation referred to the grating disc with variable contrast, and the other half of the rivalry stimulus had an orthogonal grating disc (with fixed contrast). Take the 90° for example. The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (3 cpd, 1.5° diameter, 35 cd/m^2). The contrast of the horizontal grating was fixed (1.5 log units) while the contrast of the vertical grating was varied (0-1.99 log units). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 52.5 cd/m^2), followed by the presentation of the dichoptic orthogonal grating discs (500 msec), and terminated with a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units contrast). The observer responded to his/her percept, vertical or horizontal, by key presses. If a mixture of vertical and horizontal orientation was seen, the observer would respond to the

predominant orientation. The vertical grating contrast was adjusted after each trial using the QUEST procedure (50 trials/block) until the observer obtained equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. Each block was repeated twice. When the vertical grating was presented to the LE we refer to its contrast at neutrality as the LE's balance contrast. The grating discs were then switched between the eyes to obtain the RE's balance contrast. The difference between the LE and RE balance contrast is defined as the SED.

In the pre- and post-training phases, SED was measured on four orientations. Thus, a total of 8 stimulus combinations (4 orientations x 2 eyes), in a randomized testing order, were run. During the training-phase, in order to keep the daily session within the appropriate length, we measured the SED of 0° and 45° before and after each even training session, and measured the SED of 90° and 135° before and after each odd training session.

Additionally, in the pre- and post-training phases, we measured the SED at:

a) Different contrast levels by setting the fixed contrast at 1.3 log and 1.7 log units.

We measured the SED on 0° and 45° with other stimulus parameters as same as above (3 cpd, 1.5° , 35 cd/m²). Thus, a total of 8 stimulus combinations (2 contrast levels x 2 orientations x 2 eyes), in a randomized testing order, were run.

b) Two untrained orientations of 22.5° and 67.5° (3 cpd, 1.5° , 35 cd/m², fixed contrast=1.5 log), with a total of 4 stimulus combinations (2 orientations x 2 eyes) in a randomized testing order.

c) One untrained spatial frequency of 6 cpd (0° and 45° , 1.5°, 35 cd/m², fixed contrast=1.5 log), with a total of 4 stimulus combinations (2 orientations x 2 eyes) in a randomized testing order.

Push-pull training protocol at the foveal location

As shown in Figure 6.2, a trial began with fixation at the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 52.5 cd/m²). Then a transient attention cue ($1.5^\circ \times 1.5^\circ$ frame with dash outline, width= 0.1° , 1.52 log units, 70 cd/m²) was presented monocularly to the weak eye for 100 msec (Ooi and He 1999). After a 100 msec cue-lead-time, a pair of dichoptic gratings (500 msec, 1.5°, 3cpd, 35 cd/m²) was presented. The same 100 msec cue was presented again 400 msec later, followed by a 100 msec cue-lead-time, and the presentation of a pair of dichoptic gratings (500 msec). The grating orientation shown to the weak eye in this second presentation had a slightly different orientation from the grating shown in the first presentation. Four hundred msec after the dichoptic grating presentation a binocular checkerboard sinusoidal grating mask (200 msec, $7.5^\circ \times 7.5^\circ$, 3 cpd, 35 cd/m², 1.5 log units contrast) terminated the trial. The contrast values of the dichoptic gratings were those that led to the points of neutrality in the RE and LE with the interocular imbalance test.

Before commencing the proper training phase, we determined for each observer that the cue successfully suppressed the grating viewed by the strong eye. We used a verifying test to check the perception of participants, to assure the grating in the weak eye

is 100% dominant. The stimuli for the test consisted of a pair of gratings chosen from two possible configurations, which could be, take 0° for example, either a cued horizontal grating presented to the weak eye with a vertical grating in the other eye, or a cued vertical grating presented to the weak eye with a horizontal grating in the other eye. The contrast for the vertical grating was 1.5 log units, while the contrast for the horizontal grating was the balance contrast obtained from the interocular imbalance test. One block consisted of 60 trials, with 30 trials for each configuration in a randomized order. The task for an observer was to report whether what they perceived was a vertical or a horizontal grating by pressing the corresponding key, and they should always (100%) perceive the cued grating in the weak eye, given that the cue can successfully suppress the grating in the strong eye. Indeed, we found observers' average performance to be around 95%. The observer was instructed to report by key press whether the first or second grating had a slight counterclockwise orientation, and audio feedback was given. Four orientations (0° , 45° , 90° , and 135°) with a random order were presented to the weak eye, and 25 such trials were run for each orientation in order to obtain the orientation discrimination threshold using four interleaved QUEST procedures. One experimental block consisted of four randomly interleaved QUEST runs each separately measuring the discrimination threshold of one orientation. Five blocks (100trials/block) were performed during each training day.

Figure 6.2 Push-pull training protocol at fovea. The white rectangular frame acts as a cue to attract transient attention, to cause the grating in the weak eye to be perceived while the orthogonal grating in the strong eye is suppressed. Four interleaved QUEST procedures were run to obtain the orientation discrimination thresholds of four orientations (0° , 45° , 90° , and 135°) with a random order.

Dynamics of interocular dominance and suppression

The stimulus comprised a pair of dichoptic vertical and horizontal grating discs (1.5° , 3 cpd, 35 cd/m^2 , 1.5 log units contrast) surrounded by a $7.5^\circ \times 7.5^\circ$ gray square (35 cd/m^2) (similar as shown in Figure 6.1). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 52.5 cd/m^2) and the presentation of the dichoptic orthogonal gratings (30 sec), followed by a 1 sec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.5 log units contrast). The observer's task was to report (track) his/her instantaneous percept of the binocular competitive stimulus over the 30 sec stimulus presentation. Depending on the percept, vertical, horizontal, or a mixture of both, he/she would depress the appropriate key until the next percept took over. The predominance, average duration and frequency of seeing each percept were calculated.

Two grating orientation conditions were conducted: "same grating" vs. "orthogonal grating". The same grating condition had the stimulus grating orientation presented to each eye being the same as the trained orientation of 90° . The orthogonal grating condition had the grating orientation switched between the two eyes. Altogether, there were 2 stimulus combinations (same + orthogonal). Each combination was repeated 5 times, with its order randomized.

Stereo threshold

A $7.5^\circ \times 7.5^\circ$ random-dot stereogram (dot size= 0.0132° , 35 cd/m^2) with a variable crossed-disparity disc target (1.5°) was used. The contrast of the stereogram was

individually selected for each observer, to make the stereo task moderately difficult and to avoid a possible ceiling-effect due to pixel-size constraint. (Note the smallest disparity the monitor can produce is 0.9 arc minutes.) With this criterion, the contrast levels were set at 1.0 log units for two observers, 1.1 log units for two observers, 1.2 log units for two observers, and 1.3 and 1.5 log units, respectively, for the remaining two observers.

We used the standard 2AFC method in combination with the staircase procedure to measure stereo disparity threshold. The temporal sequence of stimulus presentation was fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and random-dot mask (200 msec, $7.5^\circ \times 7.5^\circ$, 35cd/m^2). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~50-60 trials), and the last 8 reversals were taken as the average threshold. Each block was repeated 4 times, and measured over two days.

6.4 Results

1) The SED is significantly reduced at all four trained orientations, with a decrease of same balance contrast as well as an increase of orthogonal balance contrast.

First we measured the reduction of sensory eye dominance at four trained orientations (0° , 45° , 90° , and 135°). As defined in the methods section, 0° refers to the testing stimulus that consists of a pair of horizontal (0°) grating with variable contrast and orthogonal (vertical) grating with fixed contrast (1.5 log). To monitor training progress,

we measured balance contrast with the orientation of the test disc grating being either the same as or orthogonal to the orientation of the disc grating used for training. However, we predicted that the orthogonal balance contrast should also decrease since the orthogonal pair of training gratings, for example, for 0° is also the same pair of training gratings for 90° (Figure 6.1c). (Note that Figure 6.1a is the same pair of training gratings for 0° .)

The average results for four orientations are shown in Figure 6.3. Clearly, for the horizontal (0°) grating, the same balance contrast declines as the training progresses [before: slope=-0.023, $R^2=0.913$, $p=0.003$; after: slope=-0.015, $R^2=0.942$, $p=0.006$], indicating perceptual learning. What's more, as we predicted the orthogonal balance contrast also changes (increases) significantly [before: slope=0.022, $R^2=0.866$, $p=0.007$; after: slope=0.015, $R^2=0.911$, $p=0.012$]. Therefore, learning effects express as a decrease of weak eye's balance contrast as well as an increase of strong eye's balance contrast. For the 45° grating, very similar learning effect is also found [same balance contrast: before: slope=-0.024, $R^2=0.859$, $p=0.008$; after: slope=-0.012, $R^2=0.851$, $p=0.026$; orthogonal balance contrast: before: slope=0.022, $R^2=0.887$, $p=0.005$; after: slope=0.011, $R^2=0.937$, $p=0.007$]. Similar learning effect is also found for the vertical (90°) grating [same balance contrast: before: slope=-0.017, $R^2=0.805$, $p=0.015$; after: slope=-0.015, $R^2=0.908$, $p=0.012$; orthogonal balance contrast: before: slope=0.016, $R^2=0.798$, $p=0.016$; after: slope=0.011, $R^2=0.793$, $p=0.043$]. For the 135° grating, very similar learning effect is also found [same balance contrast: before: slope=-0.024, $R^2=0.781$, $p=0.019$; after:

slope=-0.019, $R^2=0.983$, $p=0.001$; orthogonal balance contrast: before: slope=0.019, $R^2=0.748$, $p=0.026$; after: slope=0.014, $R^2=0.956$, $p=0.004$].

Figure 6.3 Changes of interocular balance contrast with four orientations of 0°, 45°, 90°, and 135° showing in (a)-(d) respectively. The interocular balance contrast obtained, respectively, with grating whose orientation was the same as, or orthogonal to, the grating used in the training, and measured before and after the training every other day. Clearly, the balance contrast reduces with days in training when tested with both the same and orthogonal orientation grating for all four trained orientations.

We calculated SED, i.e., the difference between the same and orthogonal balance contrast, and Figure 6.4 plots the data obtained before and after the training session every other day. We found that SED gradually reduced with training, for all 0° (before: slope=-0.044, $R^2=0.898$, $p=0.004$; after: slope=-0.030, $R^2=0.928$, $p=0.008$), 45° (before: slope=-0.046, $R^2=0.881$, $p=0.006$; after: slope=-0.024, $R^2=0.902$, $p=0.013$), 90° (before: slope=-0.033, $R^2=0.803$, $p=0.016$; after: slope=-0.025, $R^2=0.865$, $p=0.022$), and 135° (before: slope=-0.042, $R^2=0.768$, $p=0.022$; after: slope=-0.033, $R^2=0.989$, $p=0.001$).

The learning effect of SED reduction is significant and similar under these four orientations [Main effect of training session: $F(1,7)=61.889$, $p<0.001$; main effect of orientation: $F(3,21)=0.130$, $p=0.941$; interaction effect between training session and orientation: $F(3,21)=2.374$, $p=0.099$, 2-way ANOVA with repeated measures]. Therefore, within the same training duration as used in Experiment 2, but with the exposure and training on multiple orientations, a large learning effect (similar as found in Experiment 2) is obtained on each orientation. This suggests a more efficient learning paradigm, which even works when stimuli are presented in fovea.

Figure 6.4 Changes of SED with four orientations of 0°, 45°, 90°, and 135° showing in (a)-(d) respectively. Measured both before and after the training every other day, the SED reduces significantly for all four trained orientations.

2) *Discrimination thresholds at four training orientations for the weak eye are generally reduced by perceptual training.*

There are significant improvements (decreased thresholds) on the training task of orientation discrimination for the weak eye, with different starting points and learning speed/effects at different orientations [Main effect of orientation: $F(3,21)=45.825$, $p<0.001$; main effect of training session: $F(9,63)=11.370$, $p<0.001$; interaction effect between training orientation and session: $F(27,189)=3.144$, $p<0.001$, 2-way ANOVA

with repeated measures] (Figure 6.5a). Cardinal orientations showed lower thresholds and smaller learning effects, while oblique orientations showed higher thresholds and larger learning effects (Appelle, 1972; Vandebussche, Vogels, & Orban, 1986; Sally, Poirier, & Gurnsey, 2005). Further analysis reveals a significant decrease in the threshold of all four trained orientations [0° : $F(9,36)=2.829$, $p=0.007$; 45° : $F(9,36)=5.191$, $p<0.001$; 90° : $F(9,36)=6.085$, $p<0.001$; 135° : $F(9,36)=9.144$, $p<0.001$, one-way ANOVA with repeated measures].

Figure 6.5 Changes of orientation discrimination thresholds. (a) The average orientation discrimination threshold at all four trained orientations decreases as a function of training session. (b) Orientation discrimination thresholds for 45° and 135° obtained in the last block (after) are significantly lower than those obtained in the first block (before), but insignificant before/after differences are found in discrimination thresholds for 0° and 90°.

In addition, we analyzed whether there are any before/after differences for the orientation discrimination. Since there are only five blocks in each daily training session for each orientation, we compared the first and the last block data, as plotted in Figure 6.5b. No significant before/after differences in orientation discrimination are found for cardinal orientations [Main effect of block: 0° : $F(1,7)=1.525$, $p=0.257$; 90° : $F(1,7)=2.060$, $p=0.194$, 2-way ANOVA with repeated measures]. However, orientation discrimination thresholds for oblique orientations obtained in the last block are significantly lower than those obtained in the first block [Main effect of block: 45° : $F(1,7)=46.615$, $p<0.001$; 135° : $F(1,7)=22.690$, $p=0.002$, 2-way ANOVA with repeated measures]. Furthermore, ANOVA reveals that all interaction effects fail to reach statistical significance ($p>0.1$). These findings indicate that when the task level is difficult, i.e., discriminating oblique orientations, observers' performance is getting better along with the block proceeding within a training session. Therefore, the before/after effect shown in SED (Figure 6.4) cannot be attributed to fatigue or performance deterioration. Also there is no significant correlation between the improvement of orientation discrimination and the reduction of SED during the training session (0° : $r=0.095$, $p=0.824$; 45° : $r=0.380$, $p=0.350$; 90° : $r=-0.154$, $p=0.716$; 135° : $r=0.233$, $p=0.579$), supporting the proposition that these two tasks involve distinct underlying mechanisms.

3) Large SED reductions with similar amount are shown at different contrast levels.

We also investigated the learning effect of reducing SED at different contrast levels by setting one of the paired gratings with a lower (1.3 log) or higher (1.7 log) fixed contrast. We measured learning effect on 0° and 45° (since changes on 90° and 135° can be basically inferred by the other two). We predict that the learning effect is similar at different contrast levels with the absolute values shifted linearly. And what we found is consistent with our predication (Figure 6.6). For 0° , at the 1.3 log fixed contrast level, we found a significant decrease for the same balance contrast [$t(7)=5.572$, $p=0.001$] and a significant increase for the orthogonal balance contrast [$t(7)=-4.528$, $p=0.003$]. Also at the 1.7 log fixed contrast level, similar learning effect was found [same balance contrast: $t(7)=6.389$, $p<0.001$; orthogonal balance contrast: $t(7)=-8.734$, $p<0.001$]. SED was significantly reduced at both lower [$t(7)=5.876$, $p=0.001$] and higher [$t(7)=9.259$, $p<0.001$] fixed contrast levels. The reduction in SED was similar at these three fixed contrast levels [interaction effect between contrast level and session: $F(2,14)=1.686$, $p=0.221$, 2-way ANOVA with repeated measures].

Similarly for 45° , at the 1.3 log fixed contrast level, we found a significant decrease for the same balance contrast [$t(7)=6.080$, $p=0.001$] and a significant increase for the orthogonal balance contrast [$t(7)=-5.876$, $p=0.001$]. Also at the 1.7 log fixed contrast level, a similar learning effect was found [same balance contrast: $t(7)=4.725$, $p=0.002$; orthogonal balance contrast: $t(7)=-10.975$, $p<0.001$]. SED was significantly reduced at both lower [$t(7)=9.680$, $p<0.001$] and higher [$t(7)=7.386$, $p<0.001$] fixed contrast levels. The reduction in SED was similar at these three fixed contrast levels [interaction effect

between contrast level and session: $F(2,14)=2.856$, $p=0.091$, 2-way ANOVA with repeated measures].

Figure 6.6 (a) Changes of interocular balance contrast and (b) reduction of SED at different contrast levels. (a) For 0°, equivalent learning effects are shown at both lower (1.3 log) and higher (1.7 log) contrast levels as the middle (1.5 log) contrast, with a decrease of same balance contrast and an increase of orthogonal balance contrast. Similar learning patterns are found for 45° orientation stimuli. (b) SED is reduced significantly

with equivalent amount at three fixed contrast levels (1.3, 1.5, and 1.7 log) for both 0° and 45°.

4) *The learning effect of reduced SED can be generalized to untrained orientation and spatial frequency.*

To test the generalization of the learning effects, we measured the interocular balance contrast on untrained orientations (Figure 6.7a). For 22.5°, we found a significant decrease for the weak eye balance contrast [$t(7)=6.902$, $p<0.001$] and a significant increase for the strong eye balance contrast [$t(7)=-3.946$, $p=0.006$]. Also for 67.5°, similar learning effect was found [weak eye balance contrast: $t(7)=5.892$, $p=0.001$; strong eye balance contrast: $t(7)=-10.012$, $p<0.001$]. SED was significantly reduced at both 22.5° [$t(7)=5.802$, $p=0.001$] and 67.5° [$t(7)=9.160$, $p<0.001$]. The reduction in SED was similar at these two orientations [interaction effect between orientation and session: $F(1,7)=0.081$, $p=0.784$, 2-way ANOVA with repeated measures]. To quantify the transfer effect, we calculated the mean reduction in SED of both trained and untrained orientations, by averaging results across four trained orientations and across two untrained orientations respectively; and we defined the *transfer factor* as (mean reduction in SED of untrained orientation/ mean reduction in SED of trained orientation) x 100%. We found that the mean reduction in SED of the untrained orientation (0.429 ± 0.054 log units) is comparable to the reduction of the trained orientation (0.446 ± 0.057 log units), which

leads the transfer factor to $99.634 \pm 10.318\%$. Therefore, the learning effects can be completely transferred to untrained orientations.

Figure 6.7 Learning effect of reduction in SED transfers to (a) untrained orientation and (b) untrained spatial frequency. (a) The SED is significantly reduced after the training for both 22.5° and 67.5° untrained orientation stimuli, with comparable amount to trained orientations (0° and 45°). (b) The reduction of SED also transfers to testing gratings with an untrained spatial frequency of 6 cpd, for both 0° and 45°, with similar amount to trained spatial frequency of 3 cpd.

We also measured the learning effects on the untrained spatial frequency of 6 cpd (Figure 6.7b). (Note that the weak eye does not necessarily reside in the same eye at different spatial frequency.) For 0°, we found a near significant decrease for the trained eye balance contrast [$t(7)=2.233$, $p=0.061$] and a significant increase for the suppressed eye balance contrast [$t(7)=-2.562$, $p=0.037$]. Also for 45°, similar learning effect was

found [trained eye balance contrast: $t(7)=2.017$, $p=0.084$; suppressed eye balance contrast: $t(7)=-3.144$, $p=0.016$]. SED was significantly reduced at both 0° [$t(7)=3.311$, $p=0.013$] and 45° [$t(7)=2.661$, $p=0.032$]. We also calculated the mean reduction in SED of both trained and untrained spatial frequency, by averaging results across four tested orientations of 3 cpd and across two tested orientations of 6 cpd respectively; and we defined the *transfer factor* as (mean reduction in SED of untrained frequency/ mean reduction in SED of trained frequency) $\times$ 100%. Results show that the mean reduction in SED of the untrained frequency (0.357 ± 0.117 log units) is close to the reduction of the trained frequency (0.446 ± 0.057 log units), which leads the transfer factor to $71.404 \pm 18.860\%$. Therefore, the learning effects are largely transferred to the untrained (higher) spatial frequency.

5) *The weak eye is enhanced in the dynamics of interocular dominance and suppression with both same and orthogonal stimuli conditions.*

We chose 90° (a pair of vertical and horizontal gratings) to test the consequences of reduced SED in a binocular rivalry tracking task. From the observers' tracking data, we calculated the predominance, dominance duration, suppression duration, and dominance frequency. The results are presented in Figure 6.8 as the mean ratios of the performance of the weak eye to that of the strong eye. Thus, a ratio of unity indicates the two eyes performed equally, while a ratio of greater than unity indicates the weak eye performed better for the given stimulus. Predominance: Binocular rivalry predominance ratio (weak

eye to strong eye) increases after training using both the trained orientation (same condition) and the orthogonal stimuli, with similar leaning effects [Main effect of training session: $F(1,7)=14.445$, $p=0.007$; interaction effect between stimulus orientation and session: $F(1,7)=0.734$, $p=0.420$, 2-way ANOVA with repeated measures]. Dominance duration: The dominance duration ratio (weak eye/strong eye) increases after training using both the trained orientation (same condition) and the orthogonal stimuli, with similar learning effects [Main effect of training session: $F(1,7)=39.909$, $p<0.001$; interaction effect between stimulus orientation and session: $F(1,7)=0.377$, $p=0.558$, 2-way ANOVA with repeated measures]. Suppression duration: The suppression duration ratio (weak eye/strong eye) decreases significantly after training using both the trained orientation (same condition) and the orthogonal stimuli, with similar learning effects [Main effect of training session: $F(1,7)=22.083$, $p=0.002$; interaction effect between stimulus orientation and session: $F(1,7)=0.913$, $p=0.371$, 2-way ANOVA with repeated measures]. Dominance frequency: No reliable change in dominance frequency ratio is observed after the training. We also analyzed the changes of piecemeal percept but found insignificant learning effects in predominance [same: $t(7)=-0.520$, $p=0.619$; orthogonal: $t(7)=-0.540$, $p=0.606$], dominance duration [same: $t(7)=1.249$, $p=0.252$; orthogonal: $t(7)=0.929$, $p=0.384$], and dominance frequency [same: $t(7)=-1.216$, $p=0.263$; orthogonal: $t(7)=-0.572$, $p=0.585$]. Therefore, the changes in dynamics of interocular dominance and suppression basically mirror the learning effect on SED with the measurement of a detection task.

Figure 6.8 Dynamics of interocular dominance and suppression before and after the training, measured with gratings whose orientations were either the same as, or orthogonal to, the training gratings of 90° . The data are plotted as a ratio of the performance of the weak eye to the strong eye. Thus, a ratio of greater than unity indicates a superior performance in the weak eye for that stimulus. (a) The predominance ratios are significantly increased with both the same and orthogonal gratings after the training, indicating an improvement of the weak eye. (b) The trend of the dominance duration ratios is similar to the predominance ratios. (c) The suppression duration ratios are significantly decreased with both the same and orthogonal gratings after the training,

indicating a reduction of suppression on the weak eye. (d) The dominance frequency ratios do not change significantly with training.

6) *Stereo acuity is significantly improved by perceptual training.*

As demonstrated in Figure 6.9a, the SED is significantly reduced at various orientations with a large range by the current training paradigm in this experiment. The consequence of reduced SED is also evident in the reduction of random dots stereogram disparity threshold in fovea [$t(7)=11.325$, $p<0.001$] (Figure 6.9b).

Figure 6.9 Changes of SED and stereo acuity. (a) Sketch map of the SED reduction on various orientations. (b) Binocular disparity thresholds are significantly decreased after the training.

6.5 Discussion

In the current experiment, we applied the push-pull training protocol and significantly reduced SED in fovea, contrasting with the previous three experiments in which training was implemented in parafovea. The result of foveal testing cannot be assumed without testing, as the foveal area is believed to have refined visual functions due to everyday training (Saugstadt & Lie, 1964; Frendick & Westheimer, 1983; Vogels & Orban, 1985; Ball & Sekuler, 1987). Additionally, the parafoveal area may involve extra or even different learning processing from fovea (McKee & Westheimer, 1978; Saarinen & Levi, 1994; Lu & Dosher, 2004; Nakayama & Mackeben, 1989; Beard, Levi, & Reich, 1995). However, interocular imbalance, namely SED, tested in our study is more like a status of interocular inhibitory relationship, which is relatively constant, than a performance-oriented skill, which can be improved through daily visual tasks. Our findings support our main hypothesis that with the push-pull protocol, foveal interocular imbalance can be changed through an inhibitory mechanism whereby the weak eye is stimulated repeatedly while the strong eye is suppressed at the same time.

Our last three experiments have shown stimulus-specific learning effects, which are consistent with findings in many studies on perceptual learning with various visual tasks (Fiorentini & Berardi, 1980; Ball & Sekuler, 1982; Karni & Sagi, 1991; Ahissar & Hochstein, 1993). Stimulus specificity of learning effects suggests that the loci for learning involve, but may be not limited to, early level neural networks, which are intracortical connections of interocular suppression in the visual cortex (Sengpiel &

Vorobyov, 2005). In the current experiment, we explored the generalization mechanism with the intention of extending the clinical application of our novel push-pull protocol. Researchers have been studying learning transfer for both theoretical and practical reasons. On the one hand, although there are inconsistent opinions and evidence on learning specificity and what can be inferred, e.g., whether learning happens at early neural networks exclusively (Beard et al, 1995; Schoups et al, 1995; Mollon & Danilova, 1996), specificity helps to reveal underlying mechanisms of perceptual learning (Liu, 1999; Liu & Weinshall, 2000; Xiao et al, 2008; Zhang et al, 2010). On the other hand, generalizing learning effects has obvious practical implications, and researchers have partially achieved this goal by implementing various training paradigms, such as manipulating stimulus temporal sequence (Liu & Vaina, 1998; Kuai et al, 2005; Zhang et al, 2008) and task difficulty (Ahissar & Hochstein, 1997; Linkenhoker & Knudsen, 2002; Parthasarathy, 2002). By interleaving multiple orientations with one training block, we succeeded in boosting the learning effect to all four pairs of trained orientations with the same number of training sessions and the same training duration per session as used in Experiment 2, which only trained one pair of orthogonal orientations. This suggests that there is a generic mechanism of plasticity in interocular inhibition, which is orientation independent (Xiao et al, 2008; Zhang et al, 2010). Furthermore, learning generalization occurred in that significant SED reduction also transferred to untrained gratings whose orientations are 22.5° away from trained ones or spatial frequency 1 octave above the trained one. These transfer effects are indeed in accordance with the channel theory that

spatial vision comprises a set of narrowband filters or channels to detect certain range of physical stimuli (Wilson, McFarlane, & Phillips, 1983; Watt & Morgan, 1985; Watson & Solomon, 1997). As consistently found with various experimental paradigms, orientation bandwidth is around 40° (Kulikowski, Abadi, & King-Smith, 1973; Movshon & Blakemore, 1973; Campbell & Kulikowski, 1967; Wilson & Sherman, 1976) and spatial frequency bandwidth is around 1.5 octaves (Pantle & Sekuler, 1968; Sachs, Nachmias, & Robson, 1971; Stromeyer & Julesz, 1972; Movshon, Thompson, & Tolhurst, 1978). Therefore, it was expected that we should find transfer of learning effect within half bandwidth of trained orientation or spatial frequency.

In general, the current experiment expands the theoretical significance as well as clinical implications of our push-pull training protocol in that SED can be significantly reduced even at foveal location, which is often thought over-trained already, and large changes are found at various orientations and spatial frequencies with a limited number of training sessions. First, learning and its generalization indicate that the plasticity of foveal interocular imbalance basically follows a Hebbian learning rule, and can be modified through an inhibitory mechanism. Second, the current interleaved-orientation training paradigm is more efficient than the one we used for the previous parafoveal locations, which only trains one pair of orientation at a time. What's more, significant improvement is also shown for participants' foveal stereo acuity, which is a very important binocular function but can not be fully accounted for by monocular vision enhancement. Thus, our current study provides a potential behavioral training protocol

for amblyopia patients with the goal of modifying their interocular imbalance and facilitating their binocular visual functions (e.g., stereopsis ability) at fovea, so that they can have better foveal vision for daily use.

6.5 Summary

Using the stimuli with multiple orientations interleaved within one training block, with a relative short training duration, a large learning effect of reducing SED was obtained on each orientation (Figure 6.9a). And the learning effect was similar at different contrast levels with the absolute values shifted linearly. Furthermore, the learning effect of interocular imbalance decrease was generalized to new pairs of gratings with orientations different from the training pairs, and partially transferred to untrained (higher) frequency gratings. This indicates that the “mixing-orientation” design we applied in this experiment is a more efficient learning paradigm, which works when stimuli are presented in fovea, a retinal location usually thought over-trained. In this case, the stimuli are more similar to natural scenes, and are presented to the observers’ fovea as in daily use. Learning effects were also found in changes of the dynamics of interocular dominance and suppression, and in the improvement of stereo acuity. These findings expand the clinical significance of the push-pull protocol.

CHAPTER 7

EXPERIMENT 6: PERCEPTUAL LEARNING OF BINOCULAR SUMMATION

7.1 Rationale

So far, we have investigated the perceptual learning of interocular imbalance and its underlying inhibitory mechanisms with the binocular rivalry paradigm. We have carried out a series of experiments exploring the role of attention, the contribution of boundary contours, and of learning generalization. However, little is known about the plasticity of binocular combination through summation of binocular inputs. Meese, Georgeson, and Baker (2006) proposed a two-stage model of contrast gain control, as demonstrated by Figure 7.1. In the first stage, monocular signals from each eye pass through monocular excitation and gain control (suppression), and interocular suppression, followed by binocular summation and a second stage of contrast gain control. This is largely consistent with the conceptual neural model of binocular interaction from Wilson (2003) as discussed in Experiment 2. Baker and Meese (2007) further illustrated that binocular summation is more tightly tuned than interocular suppression in both orientation and spatial frequency bandwidth. To broaden our conceptual neural model of binocular

interactions, we intended to also explore the underlying mechanisms of perceptual learning on binocular summation processing.

Figure 7.1 Schematic diagram of the two-stage model (adapted from Meese, Georgeson, & Baker, 2006). Stage 1: left and right eye signals pass through monocular excitation and binocular suppression; stage 2: binocular summation and contrast gain control. m , p , and q represent different excitatory exponents; Σ denotes summation; and grey arrows indicate divisive suppression.

In terms of important visual functions, stereopsis disparity detection involves both binocular inhibition and summation. The output stereopsis ability relies on the integration of the inputs from both eyes that cooperate together. A decrease of contrast in one eye will deteriorate stereopsis ability a nonlinear relationship (Howard & Rogers, 1995). Studies (Goodwin & Romano, 1985; Hood & Morrison, 2002) have shown high correlations between reduction of stereoacuity and reduction of both monocular and binocular visual acuity in anisometropic amblyopia, which is lack of normal binocular summation. In a recent study, Huang et al (2009) investigated suprathreshold cyclopean

perception in anisometropic amblyopia with a binocular combination paradigm developed by Ding and Sperling (2006). They found that a stimulus with equal contrast from the amblyopic eye was weighted much less than one from the fellow eye in binocular combination, regardless of differences of monocular contrast sensitivity. Due to its theoretical importance and clinical implications, in this experiment, we investigated the perceptual learning of this integration processing that includes both interocular inhibition and binocular summation, and its effect on stereopsis ability.

To accomplish our experiment goal, we applied a suprathreshold binocular combination paradigm developed by Ding and Sperling (2006) to test the binocular summation relationship. As shown in Figure 7.2, we still used a disk grating, instead of a square grating as in Ding and Sperling's study, to be consistent with previous experiments. In the test, a pair of horizontal gratings with same or different contrasts, same spatial frequency but different phases, is presented to the left and right eyes respectively, and the perceived phase is used as an index of the apparent contrast ratio between the stimuli from two eyes. During the training task, a preceding cue is presented to the weak eye, while the observer carries out a contrast discrimination task based on the grating contrast information from the weak eye. We used 1.5 log units for both the pedestal grating contrast in the weak eye and the grating contrast in the strong eye, because this is the most similar condition as in daily visual perception situation where the physical contrasts of two eyes' inputs are the same. Binocular combination and other visual functions are measured after 10-day training phase.

Figure 7.2 Four configurations used in the binocular combination test. When two sinusoidal gratings of different contrasts and phases are presented to two eyes, a cyclopean sine-wave grating with apparent contrast and phase is perceived. The higher-contrast grating can be either above the midline in the left eye (a) or right eye (b), or it can be below the midline in the left eye (c) or right eye (d). We calculated LE's binocular combination as perceived phase of (a) - (c), and RE's binocular combination as perceived phase of (b) - (d), to cancel the potential position bias.

7.2 Hypotheses

As demonstrated in Figure 3.1 (adapted from Wilson, 2003) and Figure 7.1, a conceptual neural model of binocular interaction consists of two levels: at the lower level, monocular neurons with preference of orthogonal orientations mutually inhibit each other; and at the higher level, inputs of cortical neurons with common orientation preference from the two eyes converge. In the previous experiments, through the push-pull training protocol using binocular rivalry stimuli, the strength of interocular inhibitory connections is modified, presumably with changes in synaptic efficiency, by repeated suppression of

the strong eye. In the current experiment, we intended to test the plasticity of binocular summation processing when compatible binocular stimuli are presented. Our hypothesis is that perceptual learning is going to change the weights between signals from excitatory connections, while inhibitory interneurons are hardly activated. During the training phase, we used a monocular preceding cue to attract transient, bottom-up attention to the weak eye to enhance its excitatory network repeatedly. We proposed that binocular summation can be changed through Hebbian learning rules, and that reweighted summation should increase the signal strength from the weak eye, which can balance the inputs from two eyes and facilitate stereopsis processing. We also hypothesized that monocular contrast sensitivity of the activated eye can be improved and that interocular imbalance would decrease.

7.3 Methods

7.3.1 Design

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli on a 21-inch Samsung SyncMaster flat screen CRT monitor with resolution of 2048 x 1536 at 75 Hz refresh rate (except for contrast SED, detection, and discrimination test: 1280 x 1024 at 100 Hz). Six naïve observers with clinically normal binocular vision and informed consent were tested. We capitalized on a suprathreshold binocular combination paradigm developed by Ding and Sperling (2006) to test the binocular summation relationship. In the test, a pair of horizontal grating discs

(1.5°) with same or different contrasts, and different phases (90 degrees shift) was presented to the fovea of left and right eye respectively, and the perceived phase was recorded by the method of adjustment. During the 10-day training phase, a pair of horizontal grating discs (with 90 degrees phase shift) stimulated observers' foveal location, and a preceding cue was presented to the weak eye. The observers were instructed to discriminate the grating contrast based on the grating contrast information from the weak eye (1.5 vs. 1.5+ log units) with the stimulation sequence of cue, stimulus-1, cue, stimulus-2, and mask. Binocular combination with a pair of same contrast (1.5 log units) grating discs was tested before and after each day's training session to monitor the learning progress. To further assess the learning effect, we made the following measurements at the foveal location in the pre- and post-training phases: (a) sensory eye dominance (SED); (b) stereo threshold; (c) monocular contrast detection and discrimination thresholds.

7.3.2 Observers

All six adult observers (ages 23-33) had normal or corrected-to-normal visual acuity (at least 20/20), normal color vision, clinically acceptable fixation disparity (≤ 8.6 arc min), stereopsis (≤ 20 arc sec), and passed the Keystone vision-screening test. During the experiments they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

7.3.3 Stimuli and procedure

Binocular combination test to measure perceived phase shift at fovea

The stimulus comprised a pair of horizontal sinusoidal grating discs (1.33cpd, 1.5° , 35 cd/m²) with same or different contrasts (Figure 7.2). One of the discs had 45 degrees phase shift above the midline and the other had -45 degrees phase shift below the midline, so that there was a relative phase shift (θ) of 90 degrees between them. Exactly two cycles of sinusoidal gratings were presented to each eye. In Ding and Sperling's study, they used two parameters for contrast: m , the contrast of the higher-contrast grating; δ , the fractional reduction in contrast of the lower-contrast grating. Here we employed an additive form to denote interocular contrast ratio as we are using log units to present contrast. We set a reference contrast to 1.5 log units, and adjusted ΔC chosen from three levels: 0, 0.1, and 0.2 log units. The grating contrast in one eye equaled $1.5 + \Delta C$, and the grating contrast in the other eye equaled to $1.5 - \Delta C$, which makes the interocular contrast ratio $2 \times \Delta C$ in log units. Simply, our settings of $\Delta C = 0, 0.1$, and 0.2 corresponded to the parameters of $[m, \delta] = [0.3, 1], [0.4, 0.6]$, and $[0.5, 0.4]$ in Ding and Sperling's study (with $\theta=90$ degrees). Thus, there were four configurations as demonstrated in Figure 7.2: the higher-contrast grating can be either above the midline in the left eye (a) or right eye (b), or it can be below the midline in the left eye (c) or right eye (d). Using the same way as in Huang's study, we calculated LE's binocular combination as perceived phase of (a) - (c), and RE's binocular combination as perceived phase of (b) - (d), to cancel the potential position bias. To be succinct, we used the eye with higher-contrast grating and

ΔC to refer to certain conditions. For example, condition WE_0.1 indicated the contrast setting of 1.6 log units in the weak eye and, accordingly, 1.4 log units in the strong eye. We measured the binocular combination with the both conditions of WE_ ΔC and SE_ ΔC . The perceived phase shifts from these two conditions are expected to be identical for observers who have very balanced eyes, but it is necessary to keep them separate for observers who have large interocular imbalance, i.e., SED (Ding & Sperling, 2006; Huang et al, 2009).

Figure 7.3 shows the stimulus presentation sequence. A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2) on a homogenous gray background ($7.5^\circ \times 7.5^\circ$, 35 cd/m^2), with a surrounding frame ($4^\circ \times 4^\circ$, line width= 0.1° , dash outline= 0.02 & 70 cd/m^2) to assist good binocular fusion. Observers were asked to press the “space” bar on the keyboard to indicate the stable fusion, which was followed by the presentation of a blank background (35 cd/m^2 , 500 msec) and the dichoptic horizontal grating discs. The method of adjustment was used to measure the perceived phase of the cyclopean gratings. Observers were asked to adjust the location of the horizontal reference line, whose starting position was randomized, by pressing “up” and “down” keys to indicate the apparent location of the center of the dark stripe, and press the “Enter” key after they finished the task. The trial was terminated with a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 1.33 cpd, 35 cd/m^2 , $1.5 + \Delta C$ log units contrast). A typical trial took about 5 seconds, and there were 40 trials in one block with 20 trials of higher-contrast grating phase shifts above the midline and 20 trails below the

midline, in a randomized order. Each block was repeated twice. In the pre- and post-training phases, the binocular combination (perceived phase shift) was measured at the foveal location. A total of 6 stimulus combinations ($3 \Delta C$ s x 2 eyes), in a randomized testing order, were run. During the training-phase, the binocular combination with a pair of same contrast grating discs ($\Delta C=0$) was measured before and after each day's training session.

Figure 7.3 Stimulus presentation sequence of the binocular combination test. The method of adjustment is used to measure the perceived phase of the cyclopean gratings. Observers are asked to adjust the location of the horizontal reference line to indicate the apparent location of the center of the dark stripe.

Push-pull training protocol at fovea

As presented in Figure 7.4a, a trial began with fixation at the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 52.5 cd/m^2). Then, at the foveal location, a transient attention cue ($1.5^\circ \times 1.5^\circ$ frame with dash outline, width= 0.1° , 1.52 log units, 70 cd/m^2) was presented monocularly to the weak eye for 100 msec (Ooi and He 1999). After a 100 msec cue-lead-time, a pair of dichoptic horizontal gratings (500 msec, 1.5° , 1.33cpd, 35 cd/m^2 , 1.5 log units contrast, 90 degrees relative phase shift) was presented. The same 100 msec cue was presented again 400 msec later, followed by a 100 msec cue-lead-time, and the presentation of a pair of dichoptic horizontal gratings (500 msec). The grating contrast shown to the weak eye in this second presentation had a slightly different contrast from the grating shown in the first presentation. Four hundred msec later, a binocular checkerboard sinusoidal grating mask (200 msec, $7.5^\circ \times 7.5^\circ$, 1.33 cpd, 35 cd/m^2 , 1.9 log units contrast) terminated the trial. The observer reported by key press whether the first or second grating had higher contrast, and audio feedback was given. Fifty such trials were run for each experimental block in order to obtain the contrast increment threshold using the QUEST procedure. Twelve blocks were performed during each training day.

Figure 7.4 Stimuli used in the training phase and other visual function tests. (a) Stimulus presentation sequence of a trial during training. At the foveal location, a white rectangular frame acts as a cue to attract transient attention to the grating in the weak eye.

The observer performs a contrast discrimination task based on the grating contrast information from the weak eye. (b) Horizontal and vertical gratings are used to measure the contrast SED. (c) Random-dot stereogram stimulus is used to measure binocular disparity threshold for seeing a disc target in depth. (d) Horizontal grating is used to measure monocular contrast detection threshold. (e) Horizontal grating is used to measure monocular contrast discrimination threshold.

Interocular imbalance test to measure SED at fovea

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating discs (1.33 cpd, 1.5° , 35 cd/m^2) (Figure 7.4b). We measured the SED for two orientations: 0° and 90° . Take the condition of 90° for example. The contrast of the horizontal grating was fixed (1.5 log units) while the contrast of the vertical grating was varied (0-1.99 log units). A trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width= 0.1° , 70 cd/m^2), followed by the presentation of the dichoptic orthogonal grating discs (500 msec), and terminated with a 200 msec mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 1.33 cpd, 35 cd/m^2 , 1.5 log units contrast). The observer responded to his/her percept, vertical or horizontal, by key presses. If a mixture of vertical and horizontal orientation was seen, the observer would respond to the predominant orientation. The vertical grating contrast was adjusted after each trial using the QUEST procedure (50 trials/block) until the observer obtained equal chance of seeing the vertical and horizontal gratings, i.e., the point of neutrality. Each block was repeated twice. When

the vertical grating was presented to the LE we refer to its contrast at neutrality as the LE's balance contrast. The grating discs were then switched between the eyes to obtain the RE's balance contrast. The difference between the LE and RE balance contrast is defined as the SED. The procedure for the condition of 0° was the same except that vertical grating had the fixed contrast (1.5 log units) while horizontal grating had varied contrast (0-1.99 log units). Thus, a total of 4 stimulus combinations (2 orientations x 2 eyes), in a randomized testing order, were run.

Stereo threshold at fovea

A $7.5^\circ \times 7.5^\circ$ random-dot stereogram (dot size = 0.0132° , 35 cd/m^2) with a variable crossed-disparity disc target (1.5°) was used (Figure 7.4c). The contrast of the stereogram was individually selected for each observer, to make the stereo task moderately difficult and to avoid a possible ceiling-effect due to pixel-size constraint. With this criterion, the contrast levels were set at 1.1 log units for two observers, 1.2 log units for 3 observers, and 1.5 log units for the remaining one observer.

We used the standard 2AFC method in combination with the staircase procedure to measure stereo disparity threshold. The temporal sequence of stimulus presentation was fixation, interval-1 (200 msec), blank (400 msec), interval-2 (200 msec), blank (400 msec), and random-dot mask (200 msec, $7.5^\circ \times 7.5^\circ$, 35 cd/m^2). The observer indicated whether the crossed-disparity disc was perceived in interval-1 or -2, and audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~50-60

trials), and the last 8 reversals were taken as the average threshold. Each block was repeated 4 times, and measured over two days.

Monocular contrast detection and discrimination thresholds at fovea

A monocular horizontal sinusoidal grating disc (1.5° , 1.33 cpd, 35 cd/m^2 , 500 msec) was used for the contrast detection and discrimination tasks (Figure 7.4d & e). The fellow eye viewed a homogeneous field. The test was conducted using a 2AFC method in combination with the QUEST procedure. The 2AFC stimulus presentation sequence was: fixation, interval-1 (500 msec), blank (400 msec), interval-2 (500 msec), blank (400 msec), and mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 1.33 cpd, 35 cd/m^2 , 1.5 log units, 200 msec). For the detection task, the grating was presented at only one interval while the other interval had a blank field, and the observer responded to seeing the grating either in interval-1 or -2 by key press. For the discrimination task, the pedestal contrast of the grating was 1.5 log units, and one interval had a higher (increment) contrast. The observer reported which interval had the higher contrast grating by key press. Audio feedback was given for both tasks. The grating contrast was adjusted after each trial (by QUEST) to obtain the threshold. We tested 4 stimulus combinations (2 tasks x 2 eyes) in a randomized order. Each stimulus combination was repeated over 2 blocks of trials (50 trials/block).

7.4 Results

1) Binocular combination does not show significant changes after training when $\Delta C=0$.

As we used the same contrast (1.5 log units) for both eye during the training, to monitor the training progress, we measured the binocular combination of WE_0 and SE_0 conditions ($\Delta C=0$) before and after each training session. As discussed in the method section, the perceived phase shifts from the two conditions of WE_ ΔC and SE_ ΔC are expected to be the same for observers who have very balanced binocular vision, but quite different for observers who have large interocular imbalance (Ding & Sperling, 2006; Huang et al, 2009). Thus, we kept the binocular combination of WE_0 and SE_0 calculated separately even though they have the same testing stimuli under this specific condition of $\Delta C=0$. Note that in Figure 7.2, (a)=(d) and (b)=(c) when two eyes have the same contrast. In this case, perceived phase of WE_0 and SE_0 should mirror each other with similar absolute value but opposite signs. Accordingly, when the same contrast grating discs are presented to two eyes, the perceived phase from both WE_0 and SE_0 conditions is expected to be around 0 degrees for a visual system with little interocular imbalance; however, for an observer who has a large SED, as tested in our experiments, SE_0 should obtain a positive apparent phase shift while WE_0 should obtain a negative one. During the training phase, we used a monocular preceding cue to attract transient, bottom-up attention to the weak eye to enhance its input signal repeatedly; thus, we predicted that the perceived phase would shift towards 0 degree after the training.

The average results from six participants are shown in Figure 7.5a. Surprisingly, the interocular perceived phase shows no significant changes for either the weak eye [before: slope=0.482, $R^2=0.075$, $p=0.414$, power=0.085; after: slope=-0.694, $R^2=0.241$, $p=0.150$, power=0.188] or the strong eye [before: slope=0.329, $R^2=0.065$, $p=0.450$, power=0.080; after: slope=-0.256, $R^2=0.050$, $p=0.535$, power=0.072]. There were no significant differences between before and after measurements. We calculated the power using the program G*Power 3 (Faul et al, 2007), since our results here did not reach statistical significance ($\alpha=0.05$). We got low power in some cases due to our small sample number and relatively big individual differences in terms of absolute perceived phase values. However, every observer had very similar performance trends when individual data were checked. Thus, the weak eye did not get enhanced after training.

Figure 7.5 Changes of binocular combination of $\Delta C=0$ condition. (a) Interocular perceived phase for each eye does not change over training session. The weak eye does not get strengthen in terms of perceived phase. (b) Insignificant changes are found for binocular apparent phase and imbalance phase over training session.

To consider the binocular function resulting from both eyes, we further calculated apparent phase, as used in Ding's study, i.e., $(SE+WE)/2$, and imbalance phase, i.e.,

(SE-WE), which are plotted in Figure 7.5b. As expected, neither apparent phase [before: slope=0.406, $R^2=0.198$, $p=0.170$, power=0.157; after: slope=-0.475, $R^2=0.360$, $p=0.067$, power=0.293] nor imbalance phase [before: slope=-0.153, $R^2=0.004$, $p=0.857$, power=0.052; after: slope=0.438, $R^2=0.046$, $p=0.550$, power=0.071] show significant changes. Therefore, under this push-pull training protocol, learning effects did not express with the binocular combination of $\Delta C=0$ condition, though we can not exclude other learning possibilities at this moment.

2) Learning effect is expressed with the condition of middle level interocular contrast difference as the decreased weight of the weak eye in binocular combination.

As described in the methods section, we chose the reference contrast as 1.5 log units and the interocular contrast ratio as $2x\Delta C$ log units. Simply, our settings of $\Delta C = 0, 0.1$, and 0.2 correspond to the parameters of $[m, \delta] = [0.3, 1], [0.4, 0.6]$, and $[0.5, 0.4]$ in Ding and Sperling's study (with $\theta=90$ degrees). We measured the learning effects of binocular combination at various ΔC levels (WE_ ΔC & SE_ ΔC), since binocular combination is influenced by the contrast parameters from the weak eye and the strong eye differently. We predicted that the learning effect might be shown at some ΔC level with a certain eye but not at others. Figure 7.6a displays what we found with the average data, and we plotted the data along with the decrease of interocular contrast difference ($\Delta C=0.2$ to 0 log) to make it easier to compare to the results from Ding and Sperling (2006, Figure 7.7a), and Huang et al (2009, Figure 7.7b&c). We found that the interocular perceived

phase shift significantly decreases as the interocular contrast difference (ΔC) decreases [Main effect of ΔC : $F(2,10)=257.521$, $p<0.001$, power=1.000, 3-way ANOVA with repeated measures], which is consistent with the findings from Huang et al (2009, Figure 7.7b&c). What's more, there are significant differences between the perceived phase functions for each eye, and the differences also vary at ΔC levels [Main effect of eye: $F(1,5)=12.357$, $p=0.017$, power=0.800; interaction effect between ΔC and eye: $F(2,10)=5.991$, $p=0.019$, power=0.759, 3-way ANOVA with repeated measures]. The profile of interocular perceived phase functions of observers with large imbalance in our experiment (Figure 7.6a) is more like that of amblyopic observers (Figure 7.7c) than that of normal observers (Figure 7.7b) in Huang's study.

Most importantly, the learning effects are significant but different at ΔC levels [Main effect of session: $F(1,5)=26.042$, $p=0.004$, power=0.979; interaction effect between ΔC and session: $F(2,10)=33.610$, $p<0.001$, power=1.000, 3-way ANOVA with repeated measures]. With further analysis, we found that, at the $\Delta C=0.2$ level, there are no significant changes for either the weak eye [$t(5)=0.658$, $p=0.539$, power=0.084] or the strong eye [$t(5)=1.166$, $p=0.296$, power=0.160]. However, at the $\Delta C=0.1$ level, we found a significant decrease, which is contrary to our intuition, of perceived phase in the weak eye [$t(5)=7.152$, $p=0.001$, power=0.999], but no significant changes for the strong eye [$t(5)=0.997$, $p=0.365$, power=0.129]. And at the $\Delta C=0.2$ level, no significant changes were found for either the weak eye [$t(5)=-0.337$, $p=0.750$, power=0.059] or the strong eye [$t(5)=0.600$, $p=0.575$, power=0.078].

Figure 7.6 Changes of (a) interocular perceived phase, (b) apparent phase, and (c) imbalance phase at various interocular contrast differences. Learning effect is only shown under the condition of middle level ΔC ($=0.1$) as the decreased perceived phase from the weak eye in binocular combination.

We also compared the changes of apparent phase and imbalance phase at different ΔC levels. As plotted in Figure 7.6b, we found that the apparent phase significantly decreases as the interocular contrast difference (ΔC) decreases (consistent with findings

from Ding & Sperling, 2006, Figure 7.7a), and the learning effects are significant but different at ΔC levels [Main effect of ΔC : $F(2,10)=257.521$, $p<0.001$, power=1.000; main effect of session: $F(1,5)=26.042$, $p=0.004$, power=0.979; interaction effect between ΔC and session: $F(2,10)=33.610$, $p<0.001$, power=1.000, 2-way ANOVA with repeated measures]. Further analysis reveals that there is a significant decrease of apparent phase at the $\Delta C=0.1$ level [$\Delta C=0.2$: $t(5)=1.015$, $p=0.357$, power=0.132; $\Delta C=0.1$: $t(5)=8.142$, $p<0.001$, power=0.999; $\Delta C=0$: $t(5)=0.607$, $p=0.570$, power=0.076].

For the imbalance phase (Figure 7.6c), we found that the imbalance between two eyes significantly increases as the interocular contrast difference (ΔC) decreases (consistent with findings from Huang et al, 2009), and the learning effects vary at different ΔC levels [Main effect of ΔC : $F(2,10)=5.991$, $p=0.019$, power=0.759; interaction effect between ΔC and session: $F(2,10)=4.856$, $p=0.034$, power=0.664, 2-way ANOVA with repeated measures]. Further analysis reveals that a significant increase of imbalance phase is shown only at the middle ΔC ($=0.1$) level [$\Delta C=0.2$: $t(5)=0.307$, $p=0.771$, power=0.057; $\Delta C=0.1$: $t(5)=-2.648$, $p=0.046$, power=0.568; $\Delta C=0$: $t(5)=0.497$, $p=0.640$, power=0.069]. Overall, the learning effect from our training protocol is shown at the middle level of interocular contrast different ($\Delta C=0.1$), however, as an enlarged imbalance phase with a smaller perceived phase from the weak eye, which makes the profile of interocular perceived phase functions (Figure 7.6a) more like that of amblyopic observers (Figure 7.7c).

Figure 7.7 Results adapted from Ding and Sperling (2006), and Huang et al (2009). (a) Study from Ding and Sperling shows that perceived cyclopean phase shift decreases as a function of contrast ratio δ at different m , θ levels. Parameters: m , the contrast of the higher-contrast grating; δ , the fractional reduction in contrast of the lower-contrast grating; θ , the relative phase shift between gratings in two eyes. (b) & (c) Results from Huang et al show different “phase shift versus interocular contrast ratio” functions for normal observers (b) and amblyopic observers (c).

3) Training effect is also shown as the increase of WE's balance contrast with horizontal grating; however, no significant reduction of either SED or stereo threshold is found.

We also expected that changes of binocular combination would influence the contrast interocular imbalance, i.e., sensory eye dominance (SED). We investigated the learning effects on SED at two orientations (0° and 90°). As convention, 0° (weak eye) refers to the testing stimulus that consists of a pair of horizontal (0°) grating with variable contrast (in the weak eye) and orthogonal (vertical) grating with fixed 1.5 log units contrast (in the strong eye). Because one participant has inconsistent weak eye and strong eye of binocular combination from interocular imbalance, we analyzed the data of other five participants and plotted the average result in Figure 7.8a. For 0° , we found a significant increase for the weak eye balance contrast [$t(4)=-5.228$, $p=0.006$, power=0.967] but an insignificant change for the strong eye balance contrast [$t(4)=-1.576$, $p=0.190$, power=0.235]. For 90° , there is no significant change for the weak eye balance contrast [$t(4)=1.978$, $p=0.119$, power=0.332] but a significant decrease for the strong eye balance contrast [$t(4)=2.828$, $p=0.047$, power=0.574]. Overall, there are no significant changes of SED at both 0° [$t(4)=0.116$, $p=0.913$, power=0.051] and 90° [$t(4)<0.001$, $p=1.000$, power=0.050]. These findings suggest that the balance contrast increases when the horizontal grating is presented to the weak eye (decreases when vertical grating is presented to the strong eye), which is consistent with the change found in binocular combination. This indicates the perceptual learning effect is specific to the orientation and eye-of-origin of the training stimuli.

Figure 7.8 Changes of SED and stereo acuity. (a) For 0°, the balance contrast of the weak eye significantly increases after the training; and for 90°, the balance contrast of the strong eye significantly decreases. Overall, SED does not change for both orientations. (b) There is insignificant reduction of binocular disparity threshold after the training.

To test the influence of binocular combination changes on stereopsis ability, a disparity detection task was carried out on a pair of random dots stereogram. We predicted an insignificant reduction of the stereo threshold because SED, which is the influential factor, maintained the same as shown in the results above. As we expected, we found a moderate but insignificant reduction of disparity threshold in fovea [$t(5)=2.406$, $p=0.061$, power=0.493] (Figure 7.8b). Combining the results from Figure 7.8a, it reveals that the insignificant changes of SED and disparity threshold are consistent.

4) *No systematic changes are found with monocular contrast detection or discrimination threshold.*

To explore what has been learned, we also tested monocular contrast detection and contrast discrimination (with 1.5 log units as the pedestal contrast). Our hypothesis is that under the current training protocol, what has been changed is the weight from binocular inputs, rather than monocular contrast functions. Indeed, we did not find systematic changes of monocular contrast detection or discrimination threshold (Figure 7.9a). For contrast detection, we found no significant changes on the threshold of either the weak eye [$t(5)=0.267$, $p=0.800$, power=0.057] or the strong eye [$t(5)=-0.888$, $p=0.415$, power=0.114]. Furthermore, the weak eye and strong eye have similar contrast detection thresholds before the training [$t(5)=0.053$, $p=0.960$, power=0.050] but not afterward [$t(5)=-3.436$, $p=0.019$, power=0.774]. For contrast discrimination, similar insignificant learning effects were found [weak eye: $t(5)=2.042$, $p=0.097$, power=0.350; strong eye: $t(5)=-0.003$, $p=0.998$, power=0.050], and the weak eye and strong eye also have similar contrast discrimination thresholds [pre: $t(5)=1.819$, $p=0.129$, power=0.304; post: $t(5)=-0.230$, $p=0.827$, power=0.055].

There are significant improvements (decreased thresholds) on the training task of contrast discrimination (with 1.5 log units as pedestal contrast) [$F(9,45)=3.929$, $p=0.001$, power=0.985, one-way ANOVA with repeated measures] (Figure 7.9b).

Figure 7.9 Changes of contrast detection and discrimination threshold. (a) No systematic changes are found with monocular contrast detection or discrimination threshold. (b) The average contrast increment threshold, based on the contrast information from the weak eye during training, decreases as a function of training session.

7.5 Discussion

The main concern in the current experiment is that we found insignificant learning effects in binocular combination when $\Delta C=0$, which was unexpected. There are various possible reasons, but we need to be cautious before we jump to certain conclusions, such as that the push-pull training protocol does not work for binocular combination, or “binocular summation has very distinct mechanisms from interocular inhibition”, just based on the results so far. One critical speculation in the push-pull protocol is that with the help of the preceding cue, the stimulus presented in the weak eye should be always dominant while the stimulus presented in the strong eye is suppressed during the training. In the case of binocular combination, input signals from two eyes are weighted

differently when they converge, instead of complete dominance or suppression. The interocular perceived phase of WE_0 condition should be 0 if two eyes weight equally, and is expected to be a positive value if the weak eye weights more when primed by the preceding cue during the training. Thus, we further explored the role of the preceding cue playing in the training phase, as it is critical for the learning to happen in previous experiments with the push-pull protocol. We retested five participants' interocular perceived phase of WE_0 condition both without cue (-31.994 ± 13.262 degree) and with cue (-23.494 ± 12.269 degree) by staircase procedure. We found that the perceived phase increases significantly with the help of the preceding cue [$t(4) = -3.995$, $p = 0.016$]. However, the weak eye did not weight more in binocular summation even with the cue, as its perceived phase was still negative; in contrast, the strong eye was completely suppressed in the push-pull training protocol with binocular rivalry stimuli used in previous experiments, involving interocular inhibitory mechanism. Therefore, the connotation, as well as underlying mechanism, of "push-pull protocol" applied in current experiment is largely different from what is implemented in perceptual learning of interocular inhibition.

Based on this conjecture, we propose one possible modification on the current design. We can first vary the contrast of gratings in two eyes so that ocular inputs are weighted equally when they combine, i.e., we can find the point of neutrality. Then during the training, horizontal gratings are presented respectively to two eyes in their "balance contrasts" as measured, along with a preceding cue to attract the transient attention of the

weak eye. Nevertheless, we can not exclude the possibility of null learning effect from this modified design, as binocular summation does involve different mechanisms and neural networks from interocular imbalance. It would not be surprising to find that the effective way to trigger the plasticity of excitatory connections is beyond our current push-pull training protocol.

Comparing Figure 7.6 and 7.7, we can see that we had similar findings to other studies (Ding & Sperling, 2006; Huang et al, 2009) as to the relationship between binocular combination (measured as perceived phase) and interocular contrast difference (ΔC). The interocular perceived phase shift significantly decreases as the interocular contrast difference (ΔC) decreases, and there are significant differences between the perceived phase functions for each eye, which also vary with ΔC levels. What's more, the observers with large imbalance in our experiment have very similar profile of interocular perceived phase functions to that of amblyopic observers in Huang's study. This is consistent with our conjecture that the clinical condition of amblyopia can be considered as an extreme case of excessive interocular imbalance (SED).

Our current training protocol had an effect on enlarging imbalance phase at the middle level of interocular contrast different ($\Delta C=0.1$), presumably by reducing the weight of the signal (perceived phase) from the weak eye in binocular combination, which is contrary to what we predicted. One possible explanation for this change is that the transient attention induced by the preceding cue to the weak eye enhances its input signal, so that the monocular gain control on the weak eye is increased before the

summation processing to balance the signal strength from the two eyes. With repeated training, the weight of the weak eye in binocular combination decreases over time. We suspect that with the condition of two eyes having the same contrast ($\Delta C=0$), the learning effect might get washed out by daily vision usage since the image contrasts presented to the two eyes are usually the same in most cases. When the two eyes have large interocular contrast difference ($\Delta C=0.2$), the learning effect is concealed by the high contrast in one eye, which becomes the dominant factor to drive the perceived phase shift. Furthermore, this training effect is consistently expressed in the contrast SED test as the weak eye's balance contrast increased when measured with the same (horizontal) grating as used in the training, suggesting learning specificity. We did not find significant reduction in either SED or stereo threshold. Therefore, along with the results from previous experiments, we propose that it is SED, rather than binocular combination, that has more influence on stereopsis ability.

7.6 Summary

We found that the perceived phase shift decreases as the interocular contrast difference (ΔC) decreases, and this is consistent with findings in previous studies (Ding & Sperling, 2006; Huang et al, 2009). There are basically two factors influencing binocular combination: eye imbalance and contrast difference. Under the current training protocol, the learning effect of binocular combination is (only) shown at the level of $\Delta C=0.1$ with the weak eye (having higher contrast), as the perceived phase in the weak

eye significantly decreases. This suggests the weight of the weak eye decreases in binocular summation processing at this contrast level (specifically). We also found that the balance contrast increases only when the horizontal grating is presented to the weak eye, which indicates the perceptual learning effect is specific to the orientation and eye-of-origin of the training stimuli. No significant improvement of stereo detection was found, along with the insignificant change of SED. We did not find systematic changes in monocular contrast discrimination threshold.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

8.1 Where does learning occur?

Perceptual learning is a newly rising and developing topic, which has made tremendous progress during the last several decades. More and more psychologists, neurologists and even computer scientists devote themselves to this field, not only because it is adding exciting aspects to the existing learning theories, but also because it has its own significance of understanding the plasticity and working mechanisms of mature perceptual systems. Therefore, we would like to close with some discussion on several basic questions on perceptual learning related to our current project. Since we did not find much learning effect in binocular summation, the following discussion mainly focuses on perceptual learning in interocular imbalance.

One critical question that concerns researchers is “where does perceptual leaning happen”, which is also highly relevant to the question of “what has been learned from training”. To answer this question, we need to answer another question first: what is the possible neural substrate underlying binocular rivalry which we used in current project to study the perceptual learning of interocular imbalance. As we pointed out in the

introduction section, we chose to investigate the plasticity of binocular visual system because it is a good model for exploring both excitatory and inhibitory mechanisms. Various studies from psychophysics, neurophysiology, and brain imaging (Sanderson, Bishop, & Darian-Smith, 1971; Blake & Fox, 1974; Wade & Wenderoth, 1978; Marrocco & McClurkin, 1979; Sengpiel & Blakemore, 1994; Leopold & Logothetis, 1996; Polonsky et al, 2000; Tong & Engel, 2001; Lee & Blake, 2002) have suggested that the visual stream underlying binocular rivalry suppression may have a hierarchical structure, which probably initiates from V1, or even LGN, and continues with feedback and feedforward connections to higher visual areas to complete the process (Alais & Blake, 1998; Ooi & He, 2003). With the basic sinusoidal gratings employed in our current project, we believe that the experience-dependent changes of interocular imbalance occurs at early stage of visual processing, very likely V1. This proposition is supported by our findings on learning specificity in orientation tuning, eye-of-origin, and retinal location, features of visual processing which have been considered as a signature of early cortical involvement where monocularly and the retinotopic organization of the visual input are still retained and where different orientations are processed separately (Karni & Sagi, 1991; Ahissar & Hochstein, 1993; Schoups, Vogels, & Orban, 1995; Fahle, 1997). Further evidence of stimulus-driven learning in contrast SED reduction beyond the top-down attentional focus also confirms the conjecture above (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993; Schoups et al, 2001; Watanabe, Nanez, & Sasaki, 2001; Seitz, Kim, & Watanabe, 2009). We do not expect observers would exert many cognitive

strategies to help enlarge the learning effect, since they were unaware of the experimental purpose, i.e., to reduce their sensory eye dominance, during the training of orientation or contrast discrimination task.

However, we could not assert that the modifications only happen at early visual cortex exclusively, since we did find facilitated learning effect with top-down attention deployed, especially when the testing stimuli were designed to reflex the boundary contour feature. In fact, research on perceptual learning even with simple perceptual tasks, such as contrast, orientation, or motion discrimination, has suggested that the substrates engaged in plasticity may not limit to early level neural networks (Mollon & Danilova, 1996; Liu & Weinshall, 2000; Xiao et al, 2008; Zhang et al, 2010). For example, with the double training paradigm on contrast and orientation discrimination, studies from Yu's group have suggested that perceptual learning may involve both feature learning, which is stimulus-specific, and location learning, which is stimulus-nonspecific, and may occur at different neural loci. This might raise the question of potential location transfer in our current project. We did not see this learning transfer from the push-pull location to the push-only location in Experiment 2, though it might be due to the limitation of using the monocular training stimulus at the push-only location. However, we can not completely exclude the possibility that the learning effect found at unattended location was transferred from attended location in Experiment 3, and the possibility that learning effect was transferred from the BBC location to the MBC location (or vice versa) in Experiment 4. According to the fact that different learning effects were found (with different testing

tasks) at two trained locations in both experiments, a complete location transfer is not possible, but the extent of transfer, if any, is unclear based on the current experimental design.

8.2 What is learned?

What has been learned or modified during the long-term training on reducing SED? Following from the discussion above, a short answer for this question is that reciprocal feedback inhibition between two monocular channels is learned; we can further investigate this question with relevant binocular vision models. As we have briefly reviewed before, most theories on interocular competition are similarly constructed on the basis of reciprocal inhibition (e.g., Figure 1.2 Leaky's theory), which can largely predict the properties of binocular rivalry, with the primary discrepancy in the details of their neural models to implement the proposed inhibitory mechanism (Grossberg, 1987; Wolfe, 1986; Leaky, 1988; Blake, 1989; Leaky & Blake, 1991; Wilson, Blake, & Lee, 2001; Wilson, 2003). The recent two-stage model of contrast gain control has further elaborated the binocular interactions including both inhibition and summation (Ding & Sperling, 2006; Meese, Georgeson, & Baker, 2006; Baker & Meese, 2007, Huang et al, 2009). In general, at the first stage the left and right eye channels pass through monocular excitation and gain control (suppression), and each monocular channel also exerts gain control (divisive interocular suppression) on the other channel; and then binocular summation (excitation) of left and right channels takes place before a second stage of

binocular contrast gain control. As to the plasticity of interocular imbalance focused in our project, presumably, the strength of inhibition on the weak eye from the strong eye is reduced, as well as the strength of inhibition on the strong eye from the weak eye is enhanced. This modification on inhibitory connections has its significance in both theoretical and clinical aspects, as the inhibitory network plays a critical role in the development of ocular dominance and is more dynamic than the excitatory network in adult visual cortex (Fagiolini et al, 1994; Hensch et al, 1998; Huang et al, 1999; Karmarkar & Dan, 2006; Harauzov et al, 2010). In term of the changes related to binocular summation in Experiment 6, it is possible that the monocular gain control (suppression) within the weak eye was increased by the preceding cue presented repeatedly during the training.

Another relevant question is about the time course of perceptual learning, which basically includes learning efficiency (speed), potential, and maintenance. Various time courses of perceptual learning have been noticed by researchers, implying that there are different temporal scales during the learning processes, basically divided into fast learning and slow learning (see review from Fine & Jacobs, 2000). Although some early studies suggested that fast learning usually happens with tasks involving simple neural circuits at the very early stages of perceptual pathways (Ramachandran & Braddick, 1973; Fiorentini & Berardi, 1980; Poggio, Fahle, & Edelman, 1992), the learning speed in our current project basically follows a pattern of long-term learning in that performance is improved, or SED is reduced, gradually along 7-10 daily sessions over several thousand

stimuli presented, which is similar to other perceptual learning studies with psychophysical tasks like vernier acuity, motion discrimination, and texture discrimination (Fahle & Edelman, 1993; Ball & Sekuler, 1982; Karni & Sagi, 1991, 1993). A general comparison between Experiment 2, 3 and 5 suggests that the perceptual learning in contrast SED reduction probably occurs at similar speeds in both parafovea and fovea retinal regions, though a direct comparison between the exact speeds is not possible due to specific differences between the training stimuli and procedures used in different experiments. As to the learning potential, we usually chose a retinal location with large SED (~ 0.3 log units) to train, with the intention of reducing interocular imbalance instead of enlarging the small SED to the opposite eye. Nevertheless, we did train one observer with a moderate SED (~ 0.2 log units) from the beginning, and his SED went to the opposite eye after 10-day training session. We then presented the preceding cue to his newly weak eye, and we successfully reduced his SED to a balance level. Therefore, our push-pull training protocol can exert a great learning potential of reducing interocular imbalance effectively with a relatively wide range of SED to start with.

Furthermore, the temporal aspect of perceptual learning also includes the maintenance of learning effects, and it is quite various across different task paradigms. Studies have shown that perceptual learning effects can be almost completely retained for quite a long period, ranging from days (Fiorentini & Berardi, 1980), to months (Ball & Sekuler, 1982), even up to 2-3 Years (Karni & Sagi, 1993). To evaluate the maintenance of learning effect in SED reduction, we measured observers' SED again at various

intervals (days) after the training ended in Experiment 2 (parafovea, n=10) and Experiment 5 (fovea, n=8). We averaged the SED values of four orientations (0°, 45°, 90°, and 135°) at fovea. We then calculated the maintenance as $(\text{current_SED} - \text{pre_SED}) / (\text{post_SED} - \text{pre_SED})$, so that a ratio of unity suggests a complete maintenance (Figure 8.1). It is clear that the learning effect largely maintains at both fovea and parafovea, as the maintenance is around a ratio of unity, even after months. The regression lines of maintenance along with interval basically stay horizontal, indicating no significant decrease in maintenance. This further supports the proposition that reduced SED is due to the long-term neural plasticity occurring at early visual cortex, rather than a short-term change of cognitive decision making. Additionally, it is a common phenomenon, which is also found in our study, that there are big individual differences in terms of learning efficiency, potential, and maintenance, and perceptual learning is shown by most participants and average data but for certain individuals (McKee & Westheimer, 1978; Fahle & Edelman, 1993; Beard, Levi & Reich, 1995). Possible reasons include individual plasticity of existing perceptual system, individual learning motivation, physical status, etc. We noticed that sleep (as reported by observers introspectively) has some influence on learning efficiency, which has been also suggested by other studies (Karni et al, 1994; Plihal & Born, 1999; Gais et al, 2000; Maquet, 2000, 2001; Stickgold, James, & Hobson, 2000; Siegel, 2001; Seitz et al, 2005).

Figure 8.1 Maintenance of learning effect in SED reduction at (a) fovea and (b) parafovea (each symbol represents one observer's data). Contrast SED was tested at various intervals (days) after the end of training, and maintenance is calculated the as (current_SED - pre_SED) / (post_SED - pre_SED). A ratio of unity suggests a complete maintenance. The results show learning effect largely maintains after months.

8.3 How to learn?

One significance of our study is the novel design of the push-pull training protocol, by which observers' large SED can be reduce efficiently. Based on a synaptic Hebbian learning, it can reduce the competitive advantage of the strong eye and meanwhile strengthen the weak eye, thereby, balancing two eyes. Comparing with the push-only protocol, the greater effectiveness of the push-pull protocol can be traced to the simultaneous stimulation of both excitatory and inhibitory networks to code sensory information. Inhibitory network plays a critical role in the development of visual cortex,

and especially it is more dynamic than an excitatory network in mature individuals (Hensch et al, 1998; Maffei, Nelson, & Turrigiano, 2004; Karmarkar & Dan, 2006; Harauzov et al, 2010). It is possible that the early visual cortex in adults uses the stability of excitatory network and the plasticity of the inhibitory network to control its reliability and adaptability to the environment. In this regard, even as perceptual learning is implemented by the balance between the excitatory and inhibitory networks, the learning effect is largely determined by changes in the inhibitory network (Karmarkar & Dan, 2006). This is an important difference from most previous studies on perceptual learning that mainly focus on changes in an excitatory network.

Another common question for any form of learning is to investigate the transfer of learning effects. And this is especially important for perceptual learning because it plays a significant role in revealing underlying mechanisms of perceptual learning, besides having clinical implications. By implementing an interleaved multi-orientation paradigm in the training, we generalized the learning effect on SED reduction to four orientation pairs in Experiment 5 (with 125 training trials/orientation pair/day at fovea), in contrast with the training on one orientation pair in Experiment 2 (with 600 training trials/orientation pair/day in parafovea); and the learning efficiency is very similar in these two experiments. The learning effect is also found in stimuli with different orientations and spatial frequency from the training ones. It accordingly helps to dispel our initial concern that the 500-600 push-pull training trials during daily training session in the laboratory might not be sufficient to produce a meaningful impact on the foveal

binocular visual system. Further conjecture is that there is a generic stimulus-nonspecific mechanism of plasticity in interocular inhibition, which provides an insight into the design principle to facilitate learning transfer to untrained locations, which was not shown with our current experimental setting. Possibly, this new training protocol can be applied as a post-surgery visual recovery therapy for amblyopic adults because of its efficiency and feasibility.

8.4 Relevant binocular visual functions

Our findings so far have suggested that the push-pull training protocol largely affects the interocular inhibitory neural network residing in the primary visual cortex. Since interocular inhibition is an integral part of the binocular visual processing, it is not surprising that the learning gained from the push-pull training protocol extends to other binocular visual functions besides reduced SED. Consistent with this, we have revealed the learning effect extends to binocular competition with extended viewing duration and stereo perception. Measuring SED reveals the interocular imbalance at the initial stage of interocular inhibition, while tracking the binocular competitive percept largely reveals the interocular imbalance between the eyes as they compete to maintain dominance and emerge from suppression. Despite the difference, these psychophysical tasks provide insights into the behavior of the interocular inhibitory mechanism. Consequently, we predict that a reliable correlation exists between these binocular functions and the learning effect.

To evaluate this prediction for binocular competition, we combined the data from Experiment 3 and 5, and plotted each observer's predominance ratio (SE/WE) and contrast SED in Figure 8.2a. Clearly, these two measurements vary in the same direction ($R^2=0.386$, $p<0.001$). Using the same data, we then obtained the correlation coefficient between the change in the predominance ratio (pre-post training) and the reduction in contrast SED after training. As shown in Figure 8.2b, we found a significant correlation between these two changes ($R^2=0.357$, $p=0.024$), wherein observers with more reduction in contrast SED have a larger change in their binocular competitive perception. We also examined the relationship between the reduction in stereo disparity thresholds and the reduction in contrast SED (Figure 8.2c), using the data from Experiment 2, 3, and 5. A significant correlation is found ($R^2=0.435$, $p=0.001$), indicating observers whose binocularity became more balanced (reduced SED) also have more reduction in binocular disparity threshold (improved stereoacuity).

Figure 8.2 Correlations between learning effects in relevant binocular visual functions: contrast SED, binocular competition, and stereo disparity. (a) The predominance ratio

(SE/WE) and contrast SED vary in the same direction. (b) There is a significant correlation between the change in the predominance ratio (pre-post training) and the reduction in contrast SED after training. (c) The reduction in stereo disparity thresholds highly correlates with the reduction in contrast SED.

8.5 Future directions

Although we elucidated some interesting findings in our current project, there are still many controversial and new questions worthy of future investigation. One important subject is to the potential for learning transfer between retinal locations. We did not find SED reduction at untrained locations, but as briefly discussed earlier in section 8.1, we are unclear about the extent of learning transfer between two locations when they are both presented with binocular rivalry stimulus (e.g., attended vs. unattended location, MBC vs. BBC location). We can exclude this conjecture by training two retinal locations with the push-pull protocol but using different orientation pairs; then we can test the learning transfer with the two orientation pairs (as used in the training) at both locations. However, location transfer is also possible with new experimental designs, as it has been suggested by some recent studies proposing a rule for learning through a training-plus-exposure (TPE) procedure (Xiao et al, 2008; Zhang et al, 2010). In that case, we need to further investigate the strength and duration of training and exposure necessary for a complete transfer to happen, since it is also important for clinical applications.

Another interesting issue is about the relationship between perceptual learning, adaptation, and sleep. As shown in several experiments, we found significant stimulus-specific performance deterioration after the daily training session. One possible cause is visual adaptation, which is a certain type of short-term change in terms of both function and physiology. In contrast, perceptual learning induces relatively long-term changes. So what could be the possible reasons for changes during adaptation to disappear while changes induced by perceptual learning tending to be permanent? And do they potentially interact with each other? Additionally, the usual control for the between-session periods is to maintain participants' regular daily activities without extra interventions, but it is likely sleep has some substantial influence on perceptual learning of interocular imbalance. More investigations need to be conducted on these different but related processes.

The third direction is to combine findings from behavioral studies and various neuroscience methods and techniques. On the one hand, there are comprehensive studies on underlying cellular mechanisms of brain plasticity, such as up- and down-regulation of excitatory and inhibitory transmitter systems, possible effects of growth factors, morphological reactions, and synaptic learning (LTP and LTD). The importance is to connect corresponding performance improvement with neural cellular and molecular levels, such as to investigate neurotransmitters involved in perceptual learning of interocular inhibition. On the other hand, since the stimulus-driven learning mechanism found here in the adult binocular visual system might also play a role in shaping the

ocular dominance columns formation during early binocular visual development, it would be interesting to compare the different development of the ocular dominance columns using the classic monocular deprivation paradigm versus the push-pull paradigm that excites an eye while suppressing the other eye.

Furthermore, it is obvious that we have very far to go before we understand the plasticity of binocular summation, which is probably much more complicated than originally thought. One possible modification of experimental design was proposed in the discussion section of the last experiment. Another possibility is to apply push-only (instead of push-pull) protocol to stimulate the weak eye, in order to trigger a pairing-induced plasticity, which has been demonstrated in the intact visual cortex of both cat and human (Schuett, Bonhoeffer, & Hubener, 2001; Yao & Dan, 2001).

8.6 Conclusions

Our novel push-pull training protocol, implementing repeated SE suppression along with WE dominance, successfully reduces large local SED in parafovea, with presumable modification of interocular inhibitory connections. We then illustrated that this training protocol can induce perceptual learning effectively beyond the focus of top-down attention, and that it involves BC-based processing. We further demonstrated that our push-pull protocol is equally efficient in reducing SED at the fovea, and that the learning effect can be generalized to different grating orientations. The perceptual learning of interocular imbalance focused on in our study reveals the critical role of inhibitory

mechanisms in the neural plasticity of adult visual cortex from a behavioral perspective, which has important clinical implications.

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CURRICULUM VITAE

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Education

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Department of Psychological and Brain Sciences
<i>Major Area:</i> Experimental Psychology
<i>Program:</i> Perception and Neural Sciences
<i>Specialization:</i> Vision Science	Ph.D.
2001-2005	East China Normal University
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Publications and Presentations

- Xu, J. P., He, Z. J., & Ooi, T. L. (2011). Perimetry on sensory eye dominance and its clinical implications. (In preparation)
- Xu, J. P., He, Z. J., & Ooi, T. L. (2011). Reduce sensory eye dominance (SED): Importance of suppressing signals in the strong eye during training. (In preparation)
- Xu, J. P., He, Z. J., & Ooi, T. L. (2011). Push-pull training reduces foveal sensory eye dominance within the early visual channels. *Vision Research*. (In press)
- Xu, J. P., He, Z. J., & Ooi, T. L. (2011). Perceptual learning to reduce sensory eye dominance beyond the focus of top-down visual attention. *Vision Research*. (In press)
- Xu, J. P., He, Z. J., & Ooi, T. L. (2010). Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. *Current Biology*, 20(20), 1864-1868.
- Xu, J. P., He, Z. J., & Ooi, T. L. (2010). Surface boundary contour strengthens image dominance in binocular competition. *Vision Research*, 50, 155-170.
- Xu, J. P., He, Z. J., & Ooi, T. L. (2010). Top-down attention is facilitative, but not obligatory, in perceptual learning to reduce sensory eye dominance. *Vision Sciences*

Society, Naples, FL. *Poster*

Xu, J. P., He, Z. J., & Ooi, T. L. (2009). A novel perceptual training protocol that effectively addresses both excitatory and inhibitory neural interactions in the binocular visual system. Society for Neuroscience, Chicago IL. *Talk*

Ooi, T. L., Su, Y., Xu, J., & He, Z. (2009). On boundary contour and center-surround factors in binocular rivalry [Abstract]. *Journal of Vision*, 9(8):306. *Poster*

Xu, J., He, Z. J., & Ooi, T. L. (2008). Sensory eye dominance is retinal location specific and affects stereopsis [Abstract]. *Journal of Vision*, 8(6):1089. *Talk*

Xu, J., He, Z. J., & Ooi, T. L. (2007). The roles of boundary contour and stimulus onset asynchrony in triggering binocular rivalry alternation [Abstract]. *Journal of Vision*, 7(9):61. *Poster*

Xu, J., He, Z. J., & Ooi, T. L. (2006). On the contribution of second-order boundary contour strength to binocular rivalry [Abstract]. *Journal of Vision*, 6(6): 851. *Poster*

Awards

2005-2009	Graduate Student Travel Fund, University of Louisville
2005-2007	Graduate Student Fellowship, University of Louisville
May, 2004	Students Extracurricular Academic Research Contest Award, East China Normal University
2001-2005	Student Academic Scholarship, East China Normal University

Teaching Experience

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Research Experience

2005-2011	Visual Perception and Cognition Lab, University of Louisville Research Assistant; Supervisor: Dr. Zijiang J He
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Technical Skills

Programming: VB, C, C++, MATLAB
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