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Push–pull training reduces foveal sensory eye dominance within the early visual channels

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ABSTRACT

A push–pull training protocol is applied to reduce sensory eye dominance in the foveal region. The training protocol consists of cueing the weak eye to force it to become dominant while the strong eye is suppressed when a pair of dichoptic orthogonal grating stimulus is subsequently presented to it (Ooi & He, 1999). We trained with four pairs of dichoptic orthogonal gratings (0°/90°, 90°/0°, 45°/135° and 135°/45° at 3 cpd) to affect the interocular inhibitory interaction tuned to the four trained orientations (0°, 45°, 90° and 135°). After a 10-day training session, we found a significant learning effect (reduced sensory eye dominance) at the trained orientations as well as at two other untrained orientations (22.5° and 67.5°). This suggests that the four pairs of oriented training stimuli are sufficient to produce a learning effect at any other orientation. The nearly complete transfer of the learning effect across orientation is attributed to the fact that the trained and untrained orientations are close enough to fall in the same orientation tuning function of the early visual cortical neurons (~37.5°). Applying the same notion of transfer of learning within the same feature channel, we also found a large transfer effect to an untrained spatial frequency (6 cpd), which is 1 octave higher than the trained spatial frequency (3 cpd). Furthermore, we found that stereopsis is improved, as is the competitive ability between the two eyes, after the push–pull training. Our data analysis suggests that these improvements are correlated with the reduced sensory eye dominance after the training, i.e., due to a more balanced interocular inhibition. We also found that the learning effect (reduced SED and stereo threshold) can be retained for more than a year after the termination of the push–pull training.

1. Introduction

Sensory eye dominance (SED) manifests as an unequal mutual inhibition between the two ocular channels (Ooi & He, 2001). SED can be revealed when two dissimilar dichoptic images with equal physical strength are presented to the observer to trigger the interocular inhibitory mechanism to suppress one of the two images. For observers with a significant SED, the image in the weak (non-dominant) eye is more frequently suppressed. Since equal mutual interocular inhibition is required for efficient processing of binocular information, a significant magnitude of SED can reduce stereo acuity and slow down stereo processing (Halpern & Blake, 1988; Kontsevich & Tyler, 1994; Legge & Gu, 1989; Ooi & He, 1996; Schor, 1991; Wolfe, 1986; Xu, He, & Ooi, 2010, in press). SED is not necessarily correlated with motor eye dominance, which is related to ocular dominance of perceived visual direction (Ooi & He, 2001).

Fig. 1 illustrates an example of two pairs of dichoptic test stimuli used to quantify SED. Here, in stimulus (a), the contrast of the vertical grating viewed by the right eye (RE) is fixed (constant) while the contrast of the horizontal grating viewed by the left eye (LE) is variable. During the test trial, the observer is presented with stimulus (a) for a brief interval (500 ms), and reports whether he/she sees a vertical or horizontal grating disc. Then using an adaptive procedure (QUEST), the contrast of the horizontal grating is appropriately adjusted according to the observer's report. The horizontal grating contrast is further adjusted after each subsequent trial until the observer experiences equal percentage of seeing the two gratings (point of equality). The contrast of the horizontal grating at this point of equality is referred to as the LE horizontal balance contrast. To obtain the RE horizontal balance contrast, the vertical and horizontal gratings are switched between the two eyes as in stimulus (b), and the contrast of the horizontal grating now in the RE is adjusted again until the point of equality is obtained. The difference between the LE and RE balance contrast values is defined as the SED.

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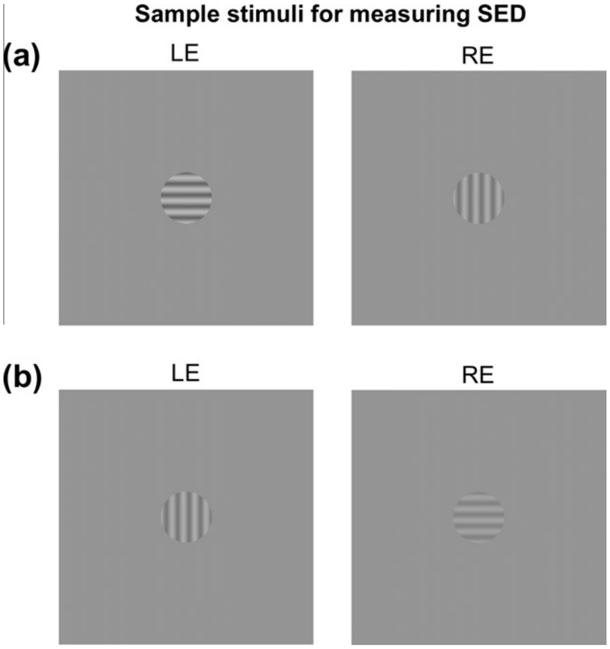

Fig. 1. Sample stimuli for measuring SED. (a) The LE balance contrast is obtained by varying the horizontal grating contrast while keeping the contrast of the vertical grating seen by the RE constant (1.5 log unit). The balance contrast is reached when the two eyes obtain an equal percentage of perceiving the two gratings (point of equality). (b) The gratings are switched between the two eyes to obtain the RE balance contrast of the horizontal grating. The difference between the LE and RE balance contrast values defines the SED.

Research on how to effectively reduce SED in adults – and thus improve binocular visual function – 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, we can use it as a model to investigate adult neural plasticity of the inhibitory cortical network and its impact on behavior (Harauzov et al., 2010; Hensch et al., 1998; Huang et al., 1999; Karmarkar & Dan, 2006). 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 the amblyopic therapy. We recently developed an approach to effectively reduce adult observers' SED using a perceptual learning protocol. Calling it the push–pull training protocol, we found that the push–pull protocol effectively reduces SED and enhances stereopsis of observers with otherwise clinically normal binocular vision (foveal stereo acuity $\leqslant$20 arcsec) (Xu et al., 2010).

Fig. 2a depicts the design of the push–pull training protocol. 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 (not shown), where only the weak eye is stimulated (push) with a visual image while the strong eye is not stimulated (no 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. This presumably reduces the strong eye's transmission efficiency and its effectiveness in suppressing the weak eye (Hebb, 1949; Xu et al., 2010), leading to reduced SED and improved stereopsis.

There are reasons to believe that the perceptual learning effect on SED with the push–pull training protocol is due to the plasticity of the primary visual cortex (V1). [The primary visual cortex as a potential site for plasticity has also been suggested by studies that investigated other aspects of perceptual learning (e.g., Fahle, 2004; Gilbert, Sigman, & Crist, 2001; Sagi & Tanne, 1994; Sasaki, Nanez, & Watanabe, 2010).] First, we observed that the reduction in SED is limited to the orientation of the stimulus (grating) used during training. A test grating orientation that is 45° away from the trained orientation elicits no change in SED after the training (Xu et al., 2010). This indicates that the perceptual learning is orientation specific, which has been considered a hallmark indicator of early cortical involvement (Fahle, 1997, 2004; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). Second, the perceptual learning effect (reduced SED and improved stereopsis) is only found at the trained retinal location (Xu et al., 2010), suggesting local neural plasticity. Third, the learning effect can be obtained without top-down attention modulation, suggesting the contribution of a stimulus-driven learning mechanism (Xu et al., in press). These findings are consistent with the spike response properties of V1 neurons, i.e., orientation selectivity with a narrow tuning function, relatively small receptive field sizes (local processing) and relatively weak top-down attention modulation (compared to neurons in the higher cortical levels) (Kastner & Ungerleider, 2000; McAdams & Maunsell, 1999; Yoshor, Ghose, Bosking, Sun, & Maunsell, 2007). Furthermore, the interocular inhibition and interactions of the signals between the two eyes (that results in SED) more likely occur in V1, where the majority of monocular neurons that carry the eye-of-origin information are found (Blake, Westendorf, & Overton, 1980; Maunsell & Van Essen, 1983; Ooi & He, 1999).

In the current report, we further reveal the impact of the learning effect on the binocular visual system with the push–pull training protocol by focusing on two issues. First, we investigated the learning effect in the foveal region. Up to now, we have only trained, and found, the learning effect in a parafoveal region (2° eccentricity). Clearly, we also need to explore whether a similar learning occurs in the foveal region since it has a prominent role in vision. We cannot simply assume that the learning should also occur in the foveal region, as perhaps, the adult visual cortex representing the peripheral retina might be more receptive to perceptual training than the foveal representation. This is because most task relevant visual information for our daily activity comes from the foveal region. In other words, the foveal representation having been overly exposed to an assortment of visual information could be less receptive to training, which requires repetitive exposures to similar information. Furthermore, even if the push–pull training protocol works in the foveal region, we need to explore if it is much more difficult to train the foveal region. This knowledge can also help us design a more efficient push–pull training protocol.

The second issue investigated in this report pertains to the generalization of the perceptual learning effect. As mentioned earlier, the primary visual cortex is probably the main site for the neural plasticity underlying the reduction in SED. Therefore, the impact of the push–pull training might be largely limited to the neurons, or neural networks (channels), tuned to the image properties of the training stimuli. However, since the ultimate goal of visual training is to reduce SED across all stimulus dimensions (properties), we have to generalize the learning effect to the neural channels whose optimal selectivity is beyond those of the training stimuli. For example, we have shown that the learning effect (reduced SED) with vertical/horizontal training stimuli does not transfer to the oblique (45°/135°) orientation (Xu et al., 2010). Consequently, to reduce SED across all orientation channels, we need to include additional training stimuli with other orientations.

How many discrete orientations do we need to train for the learning effect to benefit all orientation channels? In theory, four orientations with 45° separation in between ($180°/4 = 45°$) are