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From Imbalanced Visual Input to Imbalanced Visual Attention: Investigating the Neural Mechanisms of Short-term Ocular Dominance Plasticity

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Date: 2023-05-15T00:00:00+00:00

Abstract

During the development of the individual visual system, the structure and function of the visual system can be altered by visual experience and internal/external environmental factors, a phenomenon known as visual plasticity. Visual plasticity peaks during the postnatal critical period of development. Although the structural and functional organization of neural circuits in the adult visual cortex tends to stabilize, a growing body of research indicates that the adult visual cortex retains a certain degree of plasticity, with ocular dominance plasticity being a paradigmatic example. Studies over the past decade have demonstrated that short-term manipulation of various visual input signals in adults, and even modulation of attentional resource allocation between the two eyes, can induce shifts in adult ocular dominance. However, the neural mechanisms underlying these two forms of ocular dominance modulation may differ substantially. The regulation of adult ocular dominance by visual input may primarily reflect homeostatic plasticity mechanisms within the visual cortex, whereas the influence of attention on ocular dominance constitutes a feedback modulation from higher-level processing to the primary visual cortex, which can currently be explained by the adaptation mechanism of antagonistic neurons. Future research should seek more direct evidence to support this interpretation and should also focus on how attention and visual input interactively influence adult ocular dominance.

Full Text

From Imbalanced Visual Inputs to Imbalanced Visual Attention: Exploring the Neural Mechanisms of Short-Term Ocular Dominance Plasticity

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Abstract

During individual development, the structure and function of the visual system can be modified by visual experience and both internal and external environments, a phenomenon known as visual plasticity. Visual plasticity peaks during the critical period of postnatal development. Although the structure and function of neural circuits in the adult visual cortex tend to stabilize, mounting evidence demonstrates that the adult visual cortex retains a considerable degree of plasticity, with ocular dominance plasticity being a prime example. Over the past decade, research has shown that short-term manipulation of visual input information in adults, and even modulation of attentional resource allocation between the two eyes, can induce shifts in ocular dominance. However, the neural mechanisms underlying these two forms of modulation may differ substantially. The regulation of ocular dominance by visual input likely reflects homeostatic plasticity mechanisms within the visual cortex, whereas attentional influences on ocular dominance represent feedback modulation from higher-level processing onto primary visual cortex, currently explained by the adaptation of opponency neurons. Future research should seek more direct evidence to support this interpretation and further investigate how attention and visual input interactively influence ocular dominance in adults.

Keywords: ocular dominance, plasticity, monocular deprivation, attention

When we use our eyes to capture environmental information, both eyes typically work in concert, yet the brain's response to input from each eye is not entirely equal. In most cases, one eye produces stronger responses to visual stimuli than the other, a phenomenon known as ocular dominance, with the more responsive eye designated as the dominant eye (Porac & Coren, 1976). Common paradigms for measuring ocular dominance behaviorally include the binocular rivalry task and the binocular phase combination task. In the binocular rivalry task (Figure 1a [Figure 1: see original paper]), two incompatible images are presented separately to each eye, causing them to compete for conscious perception (Blake & Logothetis, 2002). The binocular phase combination task (Figure 1b) presents two images with different phases but compatible content to each eye, allowing

subjects to perceive an integrated image (Huang et al., 2010).

Classic neuroscience research has shown that individual ocular dominance exhibits strong plasticity during the critical period of development, being readily influenced by visual experience, but becomes largely resistant to change after this period (Wiesel & Hubel, 1963). However, numerous recent studies have revealed that the adult visual cortex retains a degree of ocular dominance plasticity (Binda et al., 2018; Kurzawski et al., 2022; Lunghi et al., 2011; Lyu et al., 2020; Menicucci et al., 2022; Min et al., 2019; Nguyen et al., 2021; Ramamurthy & Blaser, 2021; Zhou et al., 2013). For instance, Lunghi et al. (2011) found that after 150 minutes of monocular deprivation using a translucent patch (which allows light but no pattern information to reach the retina), stimuli presented to the deprived eye dominated conscious perception for longer periods in a binocular rivalry task, reflecting enhanced ocular dominance for the deprived eye—a phenomenon generally described as a shift in ocular dominance toward the deprived eye following monocular deprivation.

Subsequent research has explored factors that induce short-term ocular dominance shifts in adults to investigate the underlying mechanisms. Beyond short-term monocular patching, studies have demonstrated that ocular dominance shifts can be induced by depriving one eye of partial energy information (Yao et al., 2017; Zhou et al., 2013; Zhou et al., 2014) or by depriving one eye of Fourier phase regularity information (Bai et al., 2017; Zhou et al., 2014). Moreover, even without depriving visual input content, simply forcing attention to allocate more resources to one eye can induce ocular dominance shifts while maintaining balanced visual input between the eyes (Song et al., 2022; Wang et al., 2021).

Since the first publication on short-term ocular dominance plasticity in adults in 2011, twelve years have passed. During this period, researchers have continuously modified monocular deprivation methods, examining deprivation effects based on different types and processing levels of visual input information. This review synthesizes progress in adult monocular deprivation research, revealing the diversity of factors influencing short-term ocular dominance plasticity, highlighting the complexity of underlying neural mechanisms, and proposing directions for future exploration.

2. Effects of Short-Term Monocular Deprivation on Ocular Dominance and Its Mechanisms

The classic paradigm for studying ocular dominance plasticity is monocular patching deprivation, in which an opaque or translucent patch covers one eye for a period, after which changes in ocular dominance or visual function are observed. Results consistently show that ocular dominance shifts toward the deprived eye, with the effect magnitude typically decreasing over time after patch removal and returning to baseline levels within approximately 30-90 minutes (Chen et al., 2023; Finn et al., 2019; Lunghi et al., 2011; Sheynin et al.,

2019; Zhou et al., 2013). This patching-based deprivation eliminates nearly all visual input information, including low-level energy information and high-level contour information. This raises the question: does depriving only one type of these information categories also induce short-term ocular dominance shifts? Researchers have conducted numerous studies to address this question (Bai et al., 2017; Lyu et al., 2020; Wang et al., 2017; Yao et al., 2017; Zhou et al., 2014).

2.1 Deprivation of Energy Information from Monocular Images

When an image presented to the eye undergoes Fourier transformation, its spectrum consists of two components: amplitude spectrum and phase spectrum. The amplitude spectrum reflects energy information or contrast strength across various orientations and spatial frequencies, while the phase spectrum defines higher-order information such as contours. Traditional monocular deprivation removes all visual input information, including both energy and phase information. But does depriving only the energy information of monocular images affect ocular dominance in adults?

Regarding contrast information, Zhou et al. (2014) presented videos dichoptically to subjects, with one eye viewing the original video while the other eye viewed the same video with reduced contrast (20% or 60%). Results showed that reducing contrast to 20% induced ocular dominance shifts, whereas reduction to 60% did not, indicating that interocular differences in contrast information constitute a crucial factor driving ocular dominance changes. However, mere interocular contrast imbalance may not be a sufficient condition for inducing deprivation effects. In the same study, Zhou et al. (2014) also found that contrast-imbalanced monocular deprivation depends on spatial frequency. When one eye always viewed the original film while the other eye received stimuli with fixed contrast around 60% but deprived of either high or low spatial frequency components, deprivation of high spatial frequencies induced ocular dominance shifts toward the deprived eye after 2.5 hours, whereas deprivation of low spatial frequencies did not produce similar effects.

Regarding luminance information, research has found that 2.5 hours of monocular occlusion with either opaque or translucent patches produces similar deprivation effects, with no significant differences in effect size or duration between the two forms (Zhou et al., 2013). However, this null result does not definitively exclude the possibility that luminance deprivation contributes to ocular dominance shifts. Yao et al. (2017) found that when one eye viewed a video with constant luminance while the other eye viewed the same video with luminance reduced 1000-fold, ocular dominance shifted post-deprivation. This experimental design produced visual effects similar to Zhou et al.'s (2013) opaque occlusion study, where one eye saw the original film while the other received minimal pattern information. Yao et al. (2017) proposed that at low luminance levels, neuronal contrast gain changes (Hess, 1990; Purpura et al., 1988; Shapley & Victor, 1979), making luminance deprivation similar to contrast deprivation in

forcing adaptive adjustments in contrast gain of neurons in the deprived eye pathway, thereby producing similar monocular deprivation effects.

Regarding orientation information, Zhou et al. (2014) used the binocular phase combination task to quantify ocular dominance and found that 2.5 hours of deprivation of vertical orientation information induced significant ocular dominance shifts, increasing the spatial phase weight of the deprived eye in binocular integrated grating perception. Since the gratings used in the binocular phase combination task were horizontally oriented, deprivation of vertical information would not significantly affect horizontally orientation-selective neurons (affecting only vertically orientation-selective and non-orientation-selective neurons), yet the task still detected ocular dominance shifts, suggesting that this monocular deprivation affected non-orientation-selective neurons. To systematically investigate this, subsequent research compared ocular dominance changes after 2.5 hours of monocular deprivation of horizontal versus vertical orientation information, using both binocular combination and binocular rivalry tasks. Results showed that both orientation deprivation types induced significant ocular dominance shifts in post-tests for both tasks (Wang et al., 2017), indicating that short-term monocular deprivation effects may not be orientation-specific and primarily involve activation of orientation-insensitive neurons.

2.2 Deprivation of Phase Regularity from Monocular Images

The aforementioned experiments partially deprived image energy information and found ocular dominance shift effects similar to patching deprivation. The other component of images—phase information—encodes overall contour, structure, and positional information. Does short-term deprivation of monocular phase regularity also play a role in modulating adult ocular dominance? Researchers have addressed this question through relevant experiments (Bai et al., 2017; Lyu et al., 2020; Zhou et al., 2014).

Initially, Zhou et al. (2014) presented identical videos to both eyes while depriving phase regularity in one eye's visual input, measuring ocular dominance with the binocular phase combination task. No ocular dominance shift was observed after 2.5 hours of monocular deprivation. Subsequently, Bai et al. (2017) used both binocular rivalry and binocular phase combination tasks to further examine the effects of monocular phase regularity deprivation, finding that ocular dominance shifts could be detected with the binocular rivalry task post-deprivation. Thus, deprivation of Fourier phase regularity can modulate short-term ocular dominance, a finding corroborated by Lyu et al. (2020), who showed that after short-term deprivation of Fourier phase regularity in one eye (Figure 2 [Figure 2: see original paper]), the deprived eye dominated conscious perception for significantly longer periods in subsequent binocular rivalry. However, this deprivation form yields no detectable effect with the binocular phase combination task (Bai et al., 2017; Zhou et al., 2014), possibly because the mechanisms underlying binocular rivalry and binocular integration differ. Binocular phase integration depends critically on phase-sensitive simple cells in primary visual

cortex (Huang et al., 2010), whereas binocular rivalry involves multiple levels of the visual pathway (Tong et al., 2006), making it a more complex process. During monocular phase regularity deprivation, although contour and edge information are disrupted, simple cell activity levels remain comparable between the two eyes, minimally affecting performance in the binocular phase combination task. However, contour information substantially enhances competitive advantage in binocular rivalry (Tong et al., 2006), so deprivation of monocular phase regularity disrupts the balance in binocular rivalry, affecting the two eyes' performance. Consequently, using binocular rivalry versus binocular phase combination tasks to measure post-deprivation effects yields seemingly contradictory results.

Figure 2. Example stimuli of original and phase-scrambled images in monocular phase information deprivation experiments. The left panel shows a grayscale-processed original image presented to the non-deprived eye; the right panel shows the image presented to the deprived eye after deprivation of its phase regularity.

2.3.1 Neural Mechanism Studies

Following the discovery of short-term monocular deprivation effects in adults, numerous researchers using EEG and magnetic resonance techniques have found that short-term monocular deprivation biases neural ocular dominance in primary visual cortex toward the deprived eye (Binda et al., 2018; Lunghi, Berchicci, et al., 2015; Zhou et al., 2015).

In EEG experiments, Lunghi et al. (2015) measured visual evoked potentials generated by each eye separately before and after short-term monocular deprivation. They found that after deprivation, the amplitude of the early visual component C1 increased for the deprived eye and decreased for the non-deprived eye, with source localization analysis indicating that this early visual component originated in primary visual cortex. Additionally, researchers compared steady-state visually evoked potential (SSVEP) amplitude changes in primary visual cortex before and after monocular patching deprivation (Zhou et al., 2015). Results showed that short-term monocular patching increased SSVEP amplitude for the deprived eye without significantly changing amplitude for the non-deprived eye.

Furthermore, Lunghi et al. (2015) used magnetic resonance spectroscopy (MRS) to demonstrate that resting-state GABA concentration in primary visual cortex decreased after deprivation. Importantly, the enhancement of ocular dominance for the deprived eye correlated significantly with changes in GABA concentration. Other researchers have used functional magnetic resonance imaging (fMRI) to record blood-oxygen-level-dependent (BOLD) responses to each eye in visual cortex areas before and after monocular deprivation, finding that after 2 hours of monocular deprivation, V1 BOLD responses to the deprived eye increased significantly while responses to the non-deprived eye decreased, with

this effect extending to V2, V3, and V4 regions (Binda et al., 2018).

In summary, short-term monocular deprivation mechanisms likely involve neural activity at early stages of visual processing, with reduced GABAergic inhibition in primary visual cortex closely associated with short-term ocular dominance shifts.

2.3.2 Visual Homeostatic Plasticity Mechanism

The currently accepted explanation for short-term monocular deprivation effects is the homeostatic plasticity mechanism (Lunghi, Berchicci, et al., 2015; Turrigiano & Nelson, 2004). Homeostatic plasticity is an intrinsic mechanism that maintains normal nervous system function (Keck et al., 2017), stabilizing neuronal activity to prevent excessive hyperactivity or quiescence by returning the nervous system to baseline following perturbations (Turrigiano, 2011; Turrigiano, 1999; Turrigiano & Nelson, 2004).

Visual system homeostatic plasticity was first discovered in rodent experiments (Maffei et al., 2004), specifically showing increased visual cortex neuronal activity following monocular visual deprivation. Inspired by these animal studies, researchers tend to interpret short-term monocular deprivation-induced ocular dominance shifts in adults as resulting from homeostatic plasticity mechanisms. Specifically, when monocular deprivation creates an imbalance in visual input between the two eyes, the brain enhances neural responses in the deprived eye pathway to maintain stable neural activity across the two monocular pathways. Additionally, after monocular deprivation ends, the ocular dominance shift magnitude peaks immediately, then gradually decreases over approximately 30-90 minutes before returning to a stable baseline (Lunghi et al., 2011; Min et al., 2018; Zhou et al., 2013), a dynamic pattern consistent with homeostatic plasticity characteristics. However, homeostatic balance theory represents only a currently popular explanation for short-term monocular deprivation effects, and the actual underlying mechanisms await further exploration.

3. Attention's Influence on Short-Term Ocular Dominance Plasticity and Its Mechanisms

In the aforementioned short-term monocular deprivation studies, non-visual input factors—specifically attention—are confounded with visual deprivation. Since visual input to the deprived eye is removed, subjects obviously attend more to the non-deprived eye's images. Consequently, beyond visual input, attentional resource allocation between the two monocular pathways becomes imbalanced. Does attention, as a non-visual input factor, also influence short-term ocular dominance plasticity?

3.1 Effects of Attentional Load on Short-Term Monocular Deprivation

Addressing this question, researchers first manipulated attention during short-term monocular deprivation to explore its effects. For instance, one study investigated whether action video gaming modulates short-term monocular deprivation effects (Chen et al., 2020). Action video games require sustained attention, environmental monitoring, and rapid motor responses beyond basic audiovisual input (Bavelier & Green, 2019; Bediou et al., 2018; Dale & Shawn Green, 2017; Wong & Chang, 2018), demanding high attentional engagement. Chen et al. (2020) measured perceptual ocular dominance with the binocular phase combination task during monocular patching deprivation, comparing three conditions: playing action video games (e.g., League of Legends, Honor of Kings), playing non-action video games (e.g., Minesweeper), or watching silent action video game videos. All three conditions produced significant deprivation effects with no significant differences between them. The authors concluded that short-term ocular dominance plasticity mechanisms may be confined to early cortical pathways, influenced only by visual feedforward input rather than feedback from higher-level processes like attention.

However, this represents a statistical null result, and Chen et al.'s (2020) experimental design may not truly reflect that short-term ocular dominance plasticity is unaffected by attention. First, the study used the binocular phase combination task to measure ocular dominance, which primarily targets phase-sensitive simple cells in primary visual cortex and may ignore responses from higher-level neurons (Huang et al., 2010). Research on monocular phase regularity deprivation found deprivation effects only in binocular rivalry tasks, not in binocular phase combination tasks (Bai et al., 2017). Therefore, one possible reason Chen et al. failed to observe attention effects is suboptimal task selection. Second, the video-watching condition presented only visual images without sound, potentially requiring greater attentional investment to comprehend the video. Since Chen et al. did not objectively measure attentional levels, this remains speculative. Yet this speculation is supported by findings from a recent study that objectively measured attention during video watching (Song et al., 2022), as detailed in Section 3.2. Thus, Chen et al.'s silent video condition may have inadvertently resulted in similar attentional engagement between video-watching and action gaming conditions, yielding no difference in deprivation effects. Clearly, whether short-term ocular dominance plasticity is modulated by higher-level processes like attention requires further investigation.

3.2 Eye-Specific Attention Induces Ocular Dominance Shifts

Recent research has begun examining whether eye-specific attention alone can alter ocular dominance (Song et al., 2022; Wang et al., 2021). These studies typically maintain relatively balanced visual input between the eyes while directing attention toward one eye (eye-specific attention), creating differential attentional resource allocation, then compare ocular dominance changes after a period of attentional training. For example, Wang et al. (2021) manipulated eye-

specific attention by altering spatial structure to investigate whether it could induce ocular dominance shifts. In their study, identical images were presented to both eyes, but a Porro prism placed before one eye inverted the image vertically. Since upright images are more biologically meaningful, the researchers hypothesized subjects would selectively attend to the upright image, creating interocular attentional differences. Using binocular rivalry to measure ocular dominance, they found that after 2.5 hours of attentional training, ocular dominance shifted toward the eye viewing inverted images, suggesting eye-specific attention may modulate ocular dominance. To more directly demonstrate attention's role, their second experiment manipulated attentional engagement levels: subjects played a jigsaw puzzle game in the high-attention condition and passively watched curtains in the low-attention condition. Both monocular patching and image inversion paradigms were used, with subjects completing puzzles or watching curtains under both conditions. Results showed ocular dominance shifts only in the high-attention condition for both paradigms. Interestingly, the image inversion condition produced greater ocular dominance shifts than patching deprivation under high attention. The authors argued that the inversion condition required not only attending to the non-deprived eye's images but also suppressing the deprived eye's images, demanding greater attentional investment. In summary, Wang et al.'s (2021) study preliminarily indicates that eye-specific attention alone can induce ocular dominance shifts, biasing dominance toward the unattended eye. However, without directly measuring whether attention was preferentially allocated to upright images, attention's role in ocular dominance shifts remains inferential rather than directly evidenced.

Another paradigm for studying eye-specific attention is the "dichoptic-backward-movie" adaptation paradigm, recently introduced by Song et al. (2022). In this paradigm, subjects view normal video footage in one eye (the attended eye) while the other eye views the same video played backward in time (the unattended eye). Since backward videos are meaningless and lack logical coherence, the researchers hypothesized that to better comprehend the plot, subjects would voluntarily allocate more attention to the attended eye, creating interocular attentional differences. To manipulate attentional engagement, they established three audiovisual integration conditions: synchronous, asynchronous, and no-sound. In the synchronous condition, auditory cues matched the forward video and conflicted with the backward video, enabling easy attention to forward video through audiovisual integration (Alsius & Munhall, 2013; Lunghi et al., 2014; Vidal & Barres, 2014). In the no-sound condition, audiovisual integration assistance was removed, requiring greater effort to attend to forward video. In the asynchronous condition, sound preceded video by 5 seconds, interfering with attention to forward video. Therefore, attention to forward video should be greatest in the no-sound condition, moderate in the synchronous condition, and weakest in the asynchronous condition. Using binocular rivalry to measure ocular dominance, they found that after 60 minutes of dichoptic video viewing, ocular dominance shifted toward the unattended eye, with significantly stronger shifts in the no-sound condition than the asynchronous condition, and the syn-

chronous condition falling between them, indicating that eye-specific attention can alter ocular dominance.

Importantly, this study incorporated a target detection task during video viewing to objectively measure attentional allocation (Song et al., 2022). Targets consisted of circular regions within the video frame turning gray, appearing 24 times uniformly and randomly distributed across both eyes. Subjects pressed a button when detecting targets. Results showed significantly higher detection rates when targets appeared in the attended eye versus the unattended eye, confirming that subjects allocated more attention to the attended eye during dichoptic video viewing (Neisser & Becklen, 1975).

Beyond behavioral measures, Song et al. (2022) used SSVEP to investigate neural mechanisms of eye-specific attention-induced ocular dominance shifts. SSVEP involves tagging stimuli with flicker frequencies, with responses at those frequencies reflecting cortical responses to tagged stimuli (Norcia et al., 2015). Song et al. used SSVEP to monitor cortical responses evoked by each eye's visual input during dichoptic video viewing. In addition to interocular response differences, they examined relationships between response strengths in different brain regions, particularly between attention-related frontal regions and primary visual cortex (occipital regions). Results showed significantly stronger neural responses to attended eye input than unattended eye input, indicating attended eye dominance during video viewing. Furthermore, they found strong correlations between frontal and occipital responses: frontal responses correlated positively with occipital responses under attended conditions but negatively under unattended conditions. Finally, they found significant correlations between perceptual ocular dominance changes and frontal responses. These findings suggest that attentional allocation to the attended eye facilitates processing of its input signals in primary visual cortex while suppressing processing of unattended eye signals, making attended eye responses stronger and linking eye-specific attentional modulation to the magnitude of ocular dominance shifts, thereby providing neural-level evidence that eye-specific attention can modulate ocular dominance.

An alternative explanation exists for eye-specific attention's modulation of ocular dominance: the dichoptic backward-movie paradigm uses forward and backward video stimuli, and subjects tend to attend more to meaningful stimuli, so differences in meaningfulness between the two eyes' stimuli could differentially influence higher-level visual functions beyond attention. Thus, feedback to the two eyes might be influenced not only by attention but also by feedback from higher visual areas. However, ocular dominance shifts are unlikely to result from higher visual area feedback alone. First, if we consider higher visual function effects as consequences of attention, then higher visual area feedback would represent the influence of attentional consequences rather than attention itself. In Experiment 1 of Song et al. (2022), they compared relationships between blob detection rates and ocular dominance shifts across three audiovisual conditions, finding no direct relationship—higher blob detection rates in the syn-

chronous condition actually produced weaker ocular dominance shifts than the lower-detection-rate no-sound condition. This implies that ocular dominance changes in eye-specific attention experiments result from attention itself rather than its consequences. More importantly, Experiment 2 revealed strong SSVEP responses in frontal and occipital regions (POz, CB1, CB2) with significant correlations between them, but no notable activity in brain regions reflecting higher visual functions. Therefore, these results indicate that eye-specific attention's modulation of ocular dominance stems primarily from attention itself rather than feedback from higher visual areas.

3.3 Potential Mechanisms of Eye-Specific Attentional Modulation of Ocular Dominance

As noted, eye-specific attention can modulate interocular neural responses, making attended eye responses stronger than unattended eye responses, thereby inducing ocular dominance shifts toward the unattended eye (Song et al., 2022). This resembles short-term monocular deprivation-induced ocular dominance shifts, as both create differential neural responses between the eyes over time, shifting dominance toward the weaker eye. The first mechanism that comes to mind for explaining attention-induced ocular dominance shifts is the widely recognized homeostatic plasticity mechanism from short-term monocular deprivation research (Lunghi, Berchicci, et al., 2015; Lyu et al., 2020; Min et al., 2019; Nguyen et al., 2021). However, Song et al. (2022) found that eye-specific attention induced ocular dominance shifts only when interocular competition existed in the ocular dominance test task; no shifts occurred with binocularly fusible stimuli. This suggests that homeostatic plasticity mechanisms may not adequately explain attention-induced ocular dominance shifts. Consequently, Song et al. (2022) proposed using a binocular rivalry opponency-neuron model to explain attention-induced ocular dominance shifts.

Computational modeling of binocular rivalry proposes that opponency neurons represent interocular conflict by computing response differences between the two eyes (Said & Heeger, 2013). To accomplish this, opponency neurons receive excitatory input from one eye and inhibitory input from the other, activating only when excitatory input exceeds inhibitory input. When activated, opponency neurons suppress neural activity in the eye providing inhibitory signals through feedback mechanisms.

Song et al. (2022) proposed that attention-induced ocular dominance shifts can be explained by adaptation of opponency neurons. During video viewing, because attention is primarily directed to forward video images, neural responses in the attended eye are stronger than in the unattended eye. Consequently, opponency neurons receiving excitation from the attended eye and inhibition from the unattended eye remain activated most of the time, leading to adaptation and reduced activity. In subsequent binocular rivalry tasks, this adaptation results in weakened feedback inhibition to the unattended eye, enhancing its ocular dominance. Song et al.'s (2022) finding that minimizing interocular

competition during video viewing prevents ocular dominance shifts toward the unattended eye supports this view. Thus, opponency neuron adaptation can explain certain forms of short-term ocular dominance plasticity and may serve as an effective complement to homeostatic plasticity mechanisms.

4. Summary and Outlook

The literature reviewed above reveals distinct mechanisms through which visual input and attention influence adult ocular dominance plasticity. Visual input modulation may reflect homeostatic plasticity mechanisms at various levels of visual processing, whereas attentional modulation reflects feedback from higher-level processing onto visual processing, explainable by opponency neuron adaptation. Although progress has been made, numerous questions remain unresolved.

First, the role of eye-specific attention in short-term monocular deprivation effects must be clarified. Previous research demonstrates that eye-specific attention alone can induce ocular dominance shifts, indicating that ocular dominance is subject to attentional feedback modulation (Song et al., 2022; Wang et al., 2021). As noted, during short-term monocular deprivation, beyond visual input differences between eyes, attentional resource allocation may also differ, with the non-deprived eye receiving not only complete visual input but also greater attentional investment. Therefore, short-term monocular deprivation effects may also incorporate attentional contributions. How might attention and visual input interactively influence ocular dominance? Could increasing attention to the non-deprived eye during monocular deprivation enhance deprivation effects? Moreover, would monocular deprivation still induce ocular dominance shifts if attentional resources were balanced between the eyes? Future research could address these questions by further investigating eye-specific attention's role in short-term monocular deprivation effects.

Second, causal evidence for the relationship between eye-specific attention and ocular dominance plasticity is needed. Although previous studies have provided some neural evidence for eye-specific attention-induced ocular dominance shifts, these are insufficient due to technical limitations (Song et al., 2022). Song et al. found significant positive correlations between frontal SSVEP responses during video viewing and perceptual ocular dominance shifts, but correlation does not imply causation, so this does not directly demonstrate that eye-specific attention causes ocular dominance shifts. Future research could employ techniques such as TMS to further investigate causal relationships between eye-specific attention and ocular dominance plasticity, providing more direct evidence for attentional modulation of ocular dominance.

Third, direct neural evidence for opponency neuron adaptation mechanisms is required. Song et al. (2022) proposed opponency neuron adaptation to explain attention-induced ocular dominance shifts, but this mechanism lacks direct neural evidence. To demonstrate opponency neuron adaptation's role in attention-

induced ocular dominance shifts, they modified the dichoptic backward-movie paradigm to minimize interocular competition during video viewing, maintaining relatively equivalent activation levels of opponency neurons for both eyes and thus similar adaptation degrees. After this manipulation, ocular dominance no longer shifted post-viewing, supporting the opponency neuron adaptation mechanism. However, this key evidence is merely a null result, and they did not directly measure opponency neuron responses. Previous research has used SSVEP technology with intermodulation frequency responses as an index to demonstrate the existence of opponency neurons in visual cortex (Katyal et al., 2016; Katyal et al., 2018). Future studies could adopt this approach, using intermodulation frequency SSVEP responses as an index of opponency neuron activity to directly measure opponency neuron response strength before and after dichoptic video viewing, providing direct neural evidence for opponency neuron adaptation.

Finally, the role of opponency neuron adaptation mechanisms in short-term monocular deprivation effects requires further clarification. Song et al. (2022) proposed opponency neuron adaptation to explain attention-induced ocular dominance shifts and provided some evidence, suggesting this mechanism may explain at least certain types of short-term ocular dominance plasticity and potentially complement homeostatic plasticity mechanisms. However, opponency neuron adaptation has thus far only been applied to attention-induced ocular dominance shifts, and its applicability to more general short-term monocular deprivation effects remains unclear. Future research should further investigate opponency neuron adaptation's role in short-term monocular deprivation effects.

In conclusion, research on short-term ocular dominance plasticity in adults faces many unresolved questions. Future exploration of these issues will have important theoretical and practical implications for understanding neural plasticity mechanisms and treating eye disorders such as amblyopia.

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