Reduced Monocular Luminance Increases Monocular Temporal Synchrony Threshold in Human Adults

Ling Gong,[1] Seung Hyun Min,[2] Shijia Chen,[1] Junhan Wei,[1] Deying Kong,[1] Chunwen Tao,[1] Peng Zhang,[3] Pi-Chun Huang,[4] and Jiawei Zhou[1]

[1]School of Ophthalmology and Optometry, Affiliated Eye Hospital, State Key Laboratory of Ophthalmology, Optometry and Vision Science, Wenzhou Medical University, Wenzhou, Zhejiang, China
[2]McGill Vision Research, Department of Ophthalmology and Visual Sciences, McGill University, Montreal, Canada
[3]State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing, China
[4]Department of Psychology, National Cheng Kung University, Tainan, Taiwan

PURPOSE. The purpose of this study was to present our investigation of the influence of reduced monocular luminance on monocular and dichoptic temporal synchrony processing in healthy adults.

METHODS. Ten adults with normal or corrected to normal visual acuity participated in our psychophysical study. The temporal synchrony threshold in dichoptic (experiment 1), monocular (experiment 2), and binocular (experiment 3) viewing configurations was obtained from each observer. Four flickering Gaussian dots (one synchronous and one asynchronous pair of two dots) were displayed, from which the observers were asked to identify the asynchronous pair. The temporal phase lag in the signal pair (asynchronous) but not in the reference pair (synchronous) was varied. In addition, a neutral density (ND) filter of various intensities (1.3 and 2.0 log units) was placed before the dominant eye throughout the behavioral measurement. In the end, dichoptic, monocular, and binocular thresholds were measured for each observer.

RESULTS. With decreasing monocular luminance, the dichoptic threshold (2 ND vs. 0 ND, $P < 0.001$; 2 ND vs. 1.3 ND $P = 0.001$) and monocular threshold (2 ND vs. 0 ND, $P < 0.001$; 2 ND vs. 1.3 ND, $P = 0.003$) increased; however, the bincoular threshold remained unaffected ($P = 0.576$).

CONCLUSIONS. Reduced luminance induces delay and disturbs the discrimination of temporal synchrony. Our findings have clinical implications in visual disorders.

Keywords: luminance, temporal synchrony, monocular, delay

Luminance is important for viewing everyday visual scenes. Likewise, disrupted levels of luminance, such as unequal luminance between the eyes, can cause myriad problems in visual processing. To illustrate, reduced luminance in one eye (i.e. monocular illuminance) has been shown to perturb visual acuity[1–3] and contrast sensitivity.[4,5] It also reduces the eye's contribution in various processes of binocular vision, such as binocular combination,[6–8] binocular rivalry,[9] and depth perception.[3,10] It could naturally occur in medical conditions. For example, patients with unilateral cataracts have been shown to suffer from poor monocular perception[11] and binocular integration[12,13] because the crystalline lens from the cataracts reduce the transmission rate of visual information.[14] Peli[15] also reported that a patient with traumatic anisocoria (i.e. unequal size of the eyes' pupils) had disturbed binocular vision because the eye with

a smaller pupil size receives less light; this unequal monocular illuminance produces interocular delay (i.e. between the eyes). In addition, patients with amblyopia[16,17] or strabismus[18] have been investigated in the context of luminance; interocular suppression of the patients have been quantitatively derived from interocular luminance difference when the two eyes are balanced. Furthermore, investigators have demonstrated improvements in the binocular vision of patients with amblyopia by reducing the fellow eye's luminance in short-term viewing[8,19] and long-term training.[20,21] These previous reports collectively illustrate the clinical relevance of unequal monocular luminance.

Reduced monocular luminance produces response latency (i.e. delay in visual processing), which can mediate a string of visual phenomenon. For example, interocular delay (i.e. delay between the eyes) mediates a stereo-phenomenon

that was first studied by Carl Pulfrich and bears his name.[22,23] When no interocular delay is introduced, a moving bob of pendulum swings to and fro in the frontoparallel plane. However, by placing either the smoked glass or neutral density (ND) filter in front of one eye, the moving bob can be perceived to move in depth elliptically due to the transmission delay from the filtered eye. Therefore, depth perception occurs due to retinal disparity originating from interocular delay. In addition, there have been numerous physiological and neuroimaging studies on the effect of unequal monocular luminance. Much work has been done by measuring visual-evoked responses (VERs), revealing that reduced monocular luminance induces VER delay in the eye with an ND filter (i.e. lower luminance)[24,25] and lowers the magnitude of VER.[25–27] Moreover, accumulating evidence from magnetoencephalography (MEG)[28,29] and functional magnetic resonance imaging (fMRI) studies[30] indicates that reduced luminance prolongs response latency.

It is also well known that mean luminance affects the contrast gain of neuronal response. Purpura et al.[31] found that the contrast-gain, which is defined as a contrast-dependent change in the gain of the cell's contrast response,[32] of M cells and P cells dropped under low transmittance conditions (93.04% for M cells and 92.21% for P cells) in monkeys. The reduced contrast responses have also been shown at the striate cortex[33] and via visual-evoked responses in low luminance.[24,26,27,34] These studies demonstrate that the reduced mean luminance lowers the response amplitude, thereby highlighting another important mechanism in visual information processing at reduced illumination.

Luminance affects, but not limited to, the latency and amplitude of neural response in the visual system. The present investigation is concerned with temporal synchrony discrimination in human adults; it is the ability of the visual system to attend to temporal information by grouping common elements of an object together. In other words, the more the common elements of an object move synchronously, the more easily the visual system can process the temporal information.[35] Both the monocular and binocular visual systems have been shown to be involved in processing temporal information by grouping common elements.[36,37] In our study, we used a psychophysical task, which was introduced by Tao et al.,[38] to study the role of reduced luminance in one eye on the perception of monocular and dichoptic temporal synchrony in amblyopes. For the performance metric of observers, we estimated the threshold at which the observers could distinguish between asynchronous stimuli and synchronous stimuli. Four flickering Gaussian dots were briefly displayed, comprising two pairs of dots. One pair of dots flickered synchronously (i.e. reference pair) and the other pair asynchronously (i.e. signal pair). The subjects were asked to discriminate the signal pair of the two pairs. Throughout this paper, we refer to this ability of observers in discriminating the asynchronous pair of the stimuli dots from the synchronous counterpart as temporal synchrony threshold. The term is also synonymous with the temporal asynchrony threshold, which is the smallest degree of asynchrony that must be present in the signal pair for the observer to detect the difference between the synchronous and asynchronous stimuli. In addition, we refer to temporal synchrony threshold as the minimum time difference of the stimulus presentation between the dots within the signal pair for identification. We had hypothesized that if monocular luminance reduction induced latency between the eyes, delay could be produced. On this premise,

dichoptic but not monocular temporal synchrony from the visual stimulus itself can be disturbed. On the other hand, the latency and amplitude of neural response would not affect monocular discrimination of temporal synchrony in our task. This is because both mechanisms would not selectively affect the signal pair. Therefore, if the monocular threshold for temporal synchrony discrimination changed from reduced luminance in one eye, a new mechanism involving luminance could exist, thereby disproving the hypothesis from what we learned from the typical visual system.

METHODS

Participants

Ten adults (age: 24.1 ± 0.98 years old; 5 females) with normal or corrected-to-normal visual acuity (20/20 or better) and stereoacuity (≤ 60 arcsecs) participated in this study. All subjects had minimal (or none) degree of anisometropia (refractive error [spherical equivalent {SE}] difference ≤ 1.00 D) and astigmatism (≤ 1.00 D), and no history of eye disease or surgery. The dominant eye of each subject was determined by a pinhole test.[39] Written informed constant was obtained from each participant. The study followed the tenets of the Declaration of Helsinki and was approved by the Ethics Committee of Wenzhou Medical University.

Apparatus

The stimuli in this study were programmed with MATLAB R2015a (MathWorks, Natick, MA, USA) and the Psych-ToolBox extensions 3.0.14.[40,41] All stimuli were displayed on gamma-corrected head-mounted 3D goggles (GOOVIS Pro; NED Optics, Shenzhen, China). The resolution of the OLED goggles was 1600 × 900 pixels (corresponding to 46 × 26 degrees) and the refresh rate was 60 hertz (Hz). The maximal luminance of the goggle was 150 candela (cd)/m^2.

Stimuli

A pair of two Gaussian dots and another pair (comprising four dots total) were shown (see Fig. 1) throughout the task. One of them was above the central fixation cross, and another below. The contrast of the four dots comprising the stimulus was modulated sinusoidally at 1 Hz. The sinusoidal oscillation of the contrast refers to the fact that, on screen, the dots appeared as black at the trough of the contrast sine-wave and as white at its crest. In other words, their appearance was not static throughout the stimulus presentation. Each of the four dots was in a unique quadrant of the screen. The two dots of one pair were aligned in the diagonal axis rather than in the horizontal axis. They were separated by 2.46 degrees both horizontally and vertically, and by 4.3 degrees from the fixation cross.

One pair of the dots was the signal pair, which consisted of two dots that flickered asynchronously (i.e. the two dots in the pair had a temporal phase difference during the flicker). On the other hand, the reference pair was comprised of two dots that flickered synchronously (i.e. the two dots in the pair were phase-locked during the flicker). The four dots flickered at 1 Hz within the same time window (1 second). We introduced a temporal phase difference (i.e. temporal lag) between the dots within the signal pair to modulate the magnitude of temporal asynchrony. Moreover, to prevent participants from using local cues, we changed the SD of
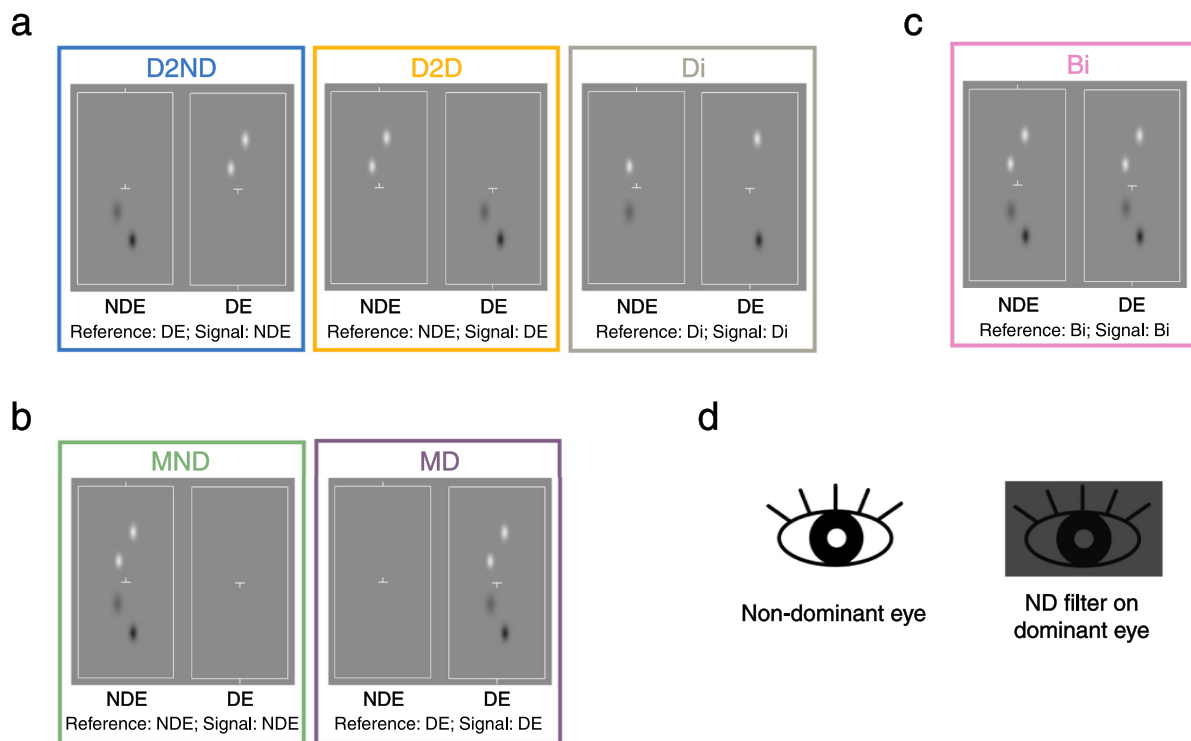
Figure 1. Illustration of the experimental design. The stimuli consisted of two pairs of Gaussian dots each flickering at 1 Hz presented at either above or below the fixation cross. A pair of two dots that flickered synchronously (phase-locked) is the reference pair (e.g. the two white dots above the fixation in this illustration), and a pair of two dots that flickered asynchronously (with different phases) is the signal pair (e.g. the two black dots in different shades below the fixation in this figure). Contrast jitters were added to the four dots across the trials, so that there was no phase-locked perception between the two pairs. The participants were asked to indicate which of the two pairs flickered asynchronously. (**a**) Experiment 1 - Dichoptic configurations. Dichoptic nondominant eye viewing configuration (D2ND), in which the signal pair was presented to the nondominant eye and the reference pair to the dominant eye; dichoptic dominant eye viewing configuration (D2D), in which the signal pair was presented to the dominant eye and the reference pair to the nondominant eye; pure dichoptic viewing configuration (Di), in which the two dots further away from the fixation cross were presented to one eye, and the remaining two closer to the fixation cross to the other eye. The order for these configurations was randomized in each luminance condition. (**b**) Experiment 2 - Monocular configurations. Monocular nondominant eye viewing configuration (MND), in which the two pair of the dots were both presented to the nondominant eye; monocular dominant eye viewing configuration (MD), in which the two pair of the dots were both presented to the dominant eye. The order for these configurations was randomized in each luminance condition. (**c**) Experiment 3 - Binocular configuration. Binocular viewing configuration (Bi), in which the signal pair and the reference pair were presented to both eyes. (**d**) The mean luminance in the nondominant eye was fixed, whereas the mean luminance of the dominant eye was varied by applying a neutral density (nominal ND) filter of various intensities: 100% (0 ND), 5% (1.3 ND), and 1% (2 ND).

the Gaussian dots from 0.28 to 0.46 degrees in a random fashion and their contrast from 40% to 80% between trials. Three dots (i.e. two dots in the reference pair and one dot in the signal pair) were phased-locked. However, because we added contrast jitters to the four dots in different trials, there was no phase-locked perception between the two pairs (see Fig. 1 for an illustration). This modification made it impossible for the participants to merely report a distinct dot of the four dots rather than a temporal synchrony.

Procedure

In this study, there were three experiments. The common aspect of all experiments was that we measured the temporal synchrony threshold, albeit in different configurations (to be described below). Throughout this paper, we refer to the temporal synchrony threshold as the minimum time difference of stimulus presentation between the dots within the signal pair for identification. Moreover, the luminance of the dominant eye was varied using a ND filter of various intensities (see Fig. 1d, and more details below) for all experiments: 0 ND (i.e. transmission rate: 100%, without ND filter), 1.3 ND

(i.e. transmission rate: 5%), and 2 ND (i.e. transmission rate: 1%). An ND filter was placed in front of the dominant eye of all subjects throughout the experiments. We randomized the order of each condition for all subjects. Before each experiment, subjects underwent a 5-minute session of light adaptation with an ND filter placed in front of their dominant eyes.

In this synchrony task, a spatial two-alternative force choice (2AFC) paradigm was adopted. Subjects were required to determine which pair of dots (above or below the central fixation cross) were flickered more asynchronously. Throughout the task, the subjects were asked to fix their gaze at the central cross, thereby making it difficult for the observers to perceive the four dots within a temporal cycle. The stimuli were presented for 1 second in each trial. The next trial started 750 milliseconds (ms) after the response of the participant.

We measured the minimum degrees of asynchrony to investigate temporal synchrony thresholds by using the method of constant stimuli. In each viewing configuration, we tested eight levels (i.e. 2, 4, 6, 8, 10, 12, 14, and 16 frames) of temporal lag (i.e. temporal phase difference between the

pair of asynchronous dots). We tested 160 trials for each viewing configuration (8 temporal lags, and 20 trials for each temporal lag). The order of eight levels of temporal lag was randomized.

In our pilot study, we used a yes/no paradigm with one-pair of dots. The results showed the proportion of yes responses deviated significantly from 50% in synchronous-pair trials for some subjects. The estimated thresholds were confounded with synchrony sensitivity and response bias.[42] Thus, we modified the design to a spatial 2AFC paradigm in order to exclude the response bias.

Experiment 1: Measurement of the Dichoptic Threshold for Temporal Synchrony Discrimination

In experiment 1, we measured the dichoptic threshold for temporal synchrony discrimination. To do so, we displayed the stimuli (the two pairs of flickering dots) in three dichoptic configurations (see Fig. 1a): (1) dichoptic nondominant eye viewing configuration (D2ND), in which the signal pair was presented to the nondominant eye and the reference pair was presented to the dominant eye; (2) dichoptic dominant eye viewing configuration (D2D), in which the signal pair was presented to the dominant eye and the reference pair was presented to the nondominant eye; (3) pure dichoptic viewing configuration (Di), in which the two dots further away from the fixation cross were presented to one eye, and the remaining two closer to the fixation cross to the other eye. The order for these configurations was randomized in each luminance condition.

Experiment 2: Measurement of the Monocular Threshold for Temporal Synchrony Discrimination

In experiment 2, we measured the monocular threshold for temporal synchrony discrimination. To do so, we displayed the stimuli (the two pair of flickering dots) in two monocular configurations (see Fig. 1b): (1) monocular nondominant eye viewing configuration (MND), in which the two pair of the dots were both presented to the nondominant eye; (2) monocular dominant eye viewing configuration (MD), in which the two pair of the dots were both presented to the dominant eye. The order for these configurations was randomized in each luminance condition.

Experiment 3: Measurement of the Binocular Threshold for Temporal Synchrony Discrimination

In experiment 3, we measured the binocular threshold for temporal synchrony discrimination. To do so, we displayed the stimuli (the two pairs of flickering dots) in a binocular viewing configuration (Bi; see Fig. 1c), in which both the signal pair and reference pair were presented to both eyes.

Data Analysis

For each configuration, the proportion correct against the temporal lag was plotted in the form of a psychometric func-

tion using Palamedes 1.8.1[43] and the following equation:

$$\psi(x; \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda)F(x; \alpha, \beta)$$
$$= \gamma + (1 - \gamma - \lambda)[1 - \exp(-(x/\alpha)^\beta)] \quad (1)$$

F $(x; \alpha, \beta)$ is a Weibull function, x is the temporal lag, α is the threshold, β is a free parameter related to the slope of the function, γ is the guessed rate, and λ is the lapse rate. The γ was set at 0.5 and λ was constrained to a fixed value (ranging from 0 to 0.06). We fitted the data from all six viewing configurations with the same luminance level simultaneously with a fixed lapse rate. According to an F-test for nested models, the full model (with different slopes across six configurations in each luminance condition) failed to generate better fits ($P > 0.05$) than the reduced model (i.e. with same slopes across six configurations) for all, but two subjects in the 2 ND condition. The latter successfully accounted for 84% ± 1% (average ± standard error), 85% ± 1% and 81% ± 2% of the variance under the 0 ND, 1.3 ND and 2 ND luminance conditions, respectively. Actually, similar thresholds and the same conclusion were found by applying the full model fitting and the reduced model fitting. We thus assumed that the slope would be the same for six configurations in each luminance condition in the fitting. The threshold and slope of the psychometric function were computed via the maximum likelihood method.

RESULTS

Experiment 1: The Effect of Reduced Monocular Luminance on the Dichoptic Threshold for Temporal Synchrony Discrimination

The dichoptic threshold for temporal synchrony discrimination was measured under three different configurations (see Fig. 1). Figure 2a shows psychometric functions, where the abscissa denotes the temporal lag (milliseconds) and the ordinate denotes the proportion correct in discriminating the signal (asynchronous) pair of the two dots (see Method). The psychometric function is plotted for each luminance condition in a different level of gray. In D2ND configuration, the goodness of fit (r^2) was 0.80 ± 0.05 (average ± standard error) under 0 ND luminance, 0.85 ± 0.02 under 1.3 ND luminance and 0.81 ± 0.02 under 2 ND luminance. In the D2D configuration, r^2 was 0.84 ± 0.04 under 0 ND luminance, 0.83 ± 0.03 under 1.3 ND luminance, and 0.76 ± 0.02 under 2 ND luminance. In Di configuration, r^2 was 0.83 ± 0.04 under 0 ND luminance, 0.81 ± 0.03 under 1.3 ND luminance, and 0.74 ± 0.04 under 2 ND luminance. The proportion of correct responses was compared across the configurations. When a 3-way repeated-measure analysis of variance (ANOVA) was performed (three levels of luminance, three levels of configuration, and eight levels of temporal lag), the effects of luminance ($F_{2,18} = 4.51$, $P = 0.026$), configuration ($F_{2,18} = 17.78$, $P < 0.001$), and temporal lag ($F_{7,63} = 251.59$, $P < 0.001$) were found to be statistically significant. The interaction was also found to be significant between configuration and temporal lag ($F_{14,126} = 2.35$, $P = 0.006$) as well as among luminance, configuration, and temporal lag ($F_{28,252} = 2.36$, $P < 0.001$).

Figure 2b shows the averaged dichoptic threshold across observers for each luminance condition. The abscissa denotes each viewing configuration of different monocular illuminance and the ordinate denotes the dichoptic thresh-
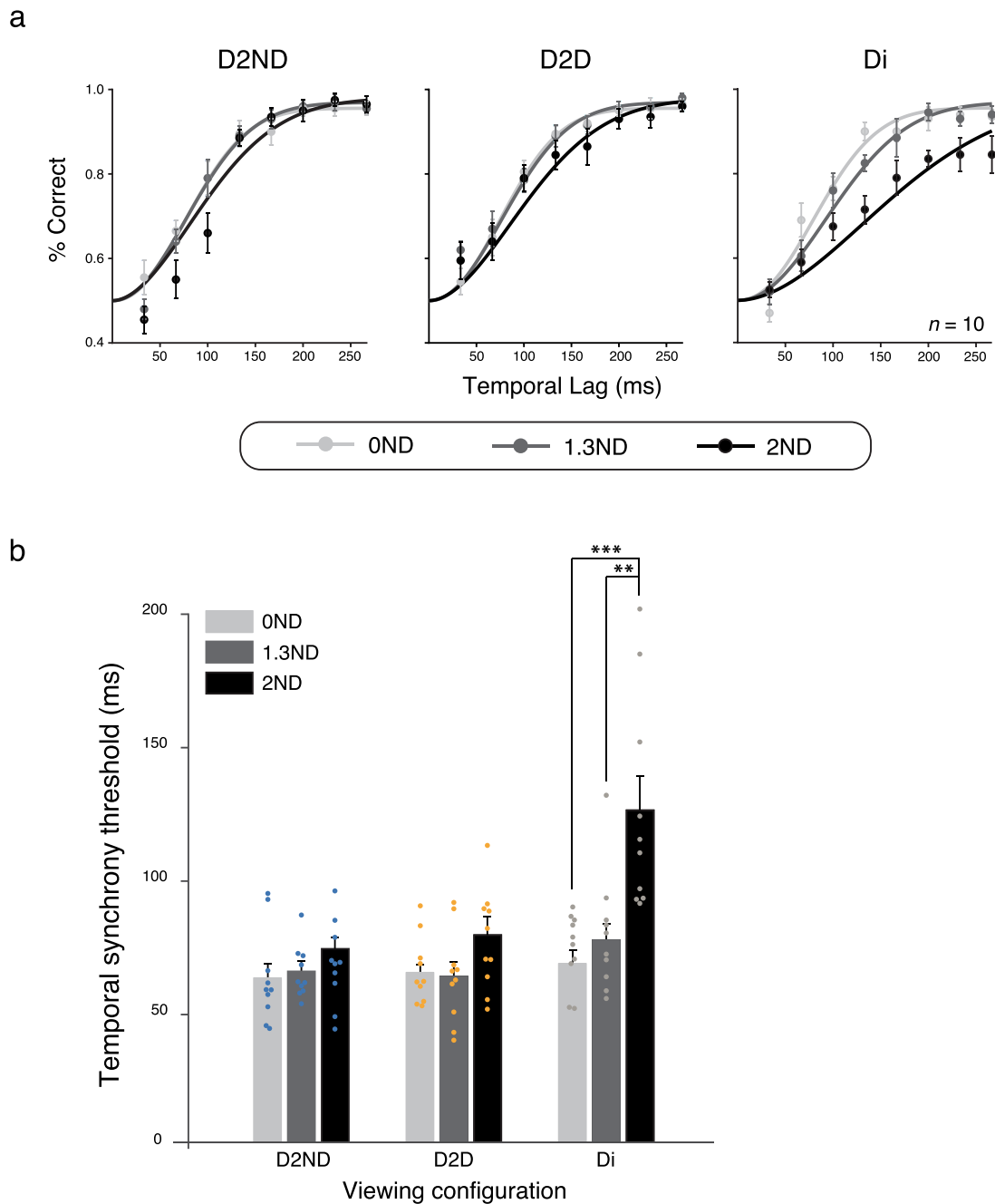
FIGURE 2. Dichoptic configurations results. (**a**) Mean psychometric functions. The proportion correct of all responses is plotted against the temporal lag. The different *shades of grey* represent different luminance conditions (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). The psychometric functions were fitted with Palamedes 1.8.1.[43] (**b**) Mean dichoptic thresholds across observers. The temporal synchrony thresholds under different configurations are illustrated. The different *shade of grey* represents different luminance conditions (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). Each solid circle represents the dichoptic threshold of one observer. Error bars represent the standard errors. ** $P < 0.01$; *** $P < 0.001$.

old for temporal synchrony discrimination (in milliseconds). Bars of different shades illustrate each luminance condition for the dominant eye, the darkest color representing the most reduced monocular luminance. To begin with, it is notable that the different levels of an ND filter placed before the dominant eye did not produce any difference in the dichoptic threshold for D2ND and D2D configurations. On the other hand, Figure 2b shows that as the filter density increases, the dichoptic threshold increases under the Di configuration (66.9 ± 4.91 ms at 0 ND, mean ± standard errors, to 124.4 ± 12.66 ms at 2 ND). These observations are confirmed by statistics. A repeated-measure ANOVA on temporal synchrony thresholds with luminance (three levels: 0 ND, 1.3 ND, and 2 ND) and dichoptic configuration (three levels: D2ND, D2D, and Di) as the within-subject factors revealed that the effects of luminance ($F_{2,18} = 11.79$, $P =$

0.001) and configuration ($F_{2,18} = 17.36$, $P < 0.001$) were significant, and that the interaction between luminance and configuration was also significant ($F_{4,36} = 7.09$, $P < 0.001$). A pairwise post hoc comparison showed a significant difference in the threshold between 2 ND and 0 ND ($P < 0.001$), as well as 2 ND and 1.3 ND ($P = 0.001$) viewing conditions under Di viewing configuration. However, we did not find a significance difference under D2ND (2 ND vs. 0 ND, $P = 0.106$; 2 ND vs. 1.3 ND, $P = 0.208$; and 1.3 ND vs. 0 ND, $P = 0.705$) and D2D (2 ND vs. 0 ND, $P = 0.076$; 2 ND vs. 1.3 ND, $P = 0.052$; 1.3 ND vs. 0 ND, $P = 0.851$) viewing configurations. In general, as the ND in the filter increased, the dichoptic threshold increased only under the Di configuration.

Experiment 2: The Effect of Reduced Monocular Luminance on the Monocular Threshold for Temporal Synchrony Discrimination

The monocular threshold for temporal synchrony discrimination was measured under two different configurations (see Fig. 1). Figure 3a shows psychometric functions, where the abscissa denotes the temporal lag (milliseconds) and the ordinate denotes the proportion correct (%) in discriminating the signal (asynchronous) pair of the two dots (see Method). The psychometric function is plotted for each luminance condition in a different level of gray. In the MND configuration, the goodness of fit (r^2) was 0.84 ± 0.03 (average $\pm$ standard error) under 0 ND luminance, 0.88 ± 0.03 under 1.3 ND luminance, and 0.88 ± 0.03 under 2 ND luminance. In MD configuration, r^2 was 0.84 ± 0.03 under 0 ND luminance, 0.86 ± 0.03 under 1.3 ND luminance, and 0.78 ± 0.03 under 2 ND luminance. The proportion of correct responses was compared. The effects of configuration ($F_{1,9} = 7.63$, $P = 0.022$) and temporal lag were found to be significant ($F_{7,63} = 194.86$, $P < 0.001$) from a 3-way repeated-measure ANOVA (three levels of luminance, two levels of configuration, and eight levels of temporal lag). Moreover, the effect of luminance was found to be not significant ($F_{2,18} = 1.85$, $P = 0.186$). In addition, interaction was found to be significant between the configurations and the luminance ($F_{2,18} = 4.48$, $P = 0.026$).

Figure 3b shows the averaged monocular threshold across observers for each luminance condition. The abscissa denotes each viewing configuration of different monocular illuminance and the ordinate denotes the monocular threshold for temporal synchrony discrimination (milliseconds). Bars of different shades illustrate each luminance condition for the dominant eye, the darkest color representing the most reduced monocular luminance. To begin with, it is evident that the different levels of an ND filter placed before the dominant eye did not produce any difference in the monocular threshold for the MND configuration. On the other hand, it is clear that as the filter density increases, the monocular threshold increases under the MD configuration (55.3 ± 2.96 ms at 0 ND to 92.2 ± 6.91 ms at 2 ND). These observations are confirmed by statistics. A repeated-measure ANOVA on the monocular threshold with luminance (three levels: 0 ND, 1.3 ND, and 2 ND) and configuration (two levels: MND and MD) as the within-subject factors revealed that the effect of luminance ($F_{2,18} = 12.22$, $P < 0.001$) and configuration ($F_{1,9} = 10.36$, $P = 0.011$) were significant. The interaction between luminance and configuration was also significant ($F_{2,18} = 6.35$, $P = 0.008$). A pairwise post hoc

comparison found that the monocular threshold difference was significant between 2 ND vs. 0 ND ($P < 0.001$) and 2 ND vs. 1.3 ND ($P = 0.003$) under the MD configuration, but not so under the MND (2 ND vs. 0 ND, $P = 0.553$; 2 ND vs. 1.3 ND, $P = 0.553$; and 1.3 ND vs. 0 ND, $P = 0.976$) configuration. In short, as the ND in the filter increased, the monocular threshold increased only under the MD configuration.

Experiment 3: The Effect of Reduced Monocular Luminance on the Binocular Threshold for Temporal Synchrony Discrimination

The binocular threshold for temporal synchrony discrimination was measured in one binocular configuration (see Fig. 1; Bi). Figure 4a shows psychometric functions, where the abscissa denotes the temporal lag (milliseconds) and the ordinate denotes the proportion correct (%) in discriminating the signal (asynchronous) pair of the two dots (see Method). The psychometric function is plotted for each luminance condition in a different level of gray. In Bi configuration, the goodness of fit (r^2) was 0.86 ± 0.02 (average $\pm$ standard error) under 0 ND luminance, 0.85 ± 0.03 under 1.3 ND luminance, and 0.89 ± 0.02 under 2 ND luminance. The proportion of correct responses was compared. The effect of temporal lag was found to be significant ($F_{2.8,24.8} = 303.72$, $P < 0.001$) from a 2-way repeated-measure ANOVA (three levels of luminance and eight levels of temporal lag as within-subject factors). The effect of luminance was not significant ($F_{2,18} = 0.67$, $P = 0.525$). No interaction effect between luminance and temporal lag ($F_{4.3,38.8} = 1.28$, $P = 0.232$) was found.

Figure 4b shows the averaged binocular threshold across observers. The abscissa denotes viewing configuration of different monocular illuminance and the ordinate denotes the binocular threshold for temporal synchrony discrimination (milliseconds). Bars of different shades illustrate each luminance condition for the dominant eye, the darkest color representing the most reduced monocular luminance. In Figure 4b, it is evident that the different levels of an ND filter placed before the dominant eye did not produce any difference in the binocular threshold for the Bi configuration. This observation is verified by statistics. A 1-way ANOVA found no difference of the binocular threshold across the three viewing conditions ($F_{2,27} = 0.56$, $P = 0.576$). In sum, as the ND in the filter increased, the binocular threshold did not increase under the Bi configuration.

Our findings demonstrate that the increase in the ND of the filter elevates the dichoptic and monocular thresholds (from the Di and MD configurations, respectively). To examine the relationship between the increased dichoptic threshold (from the Di configuration) and the increased monocular threshold (from the MD configuration), the effect of reduced monocular luminance was computed; the thresholds in 2 ND was divided by the thresholds in 0 ND. Then the increase of the dichoptic threshold was plotted against the increase of the monocular threshold. Figure 5 illustrates the correlation, where the abscissa represents the proportion of the increase in the monocular threshold, and the ordinate represents the proportion of the increase in the dichoptic threshold. A two-tailed Pearson correlation analysis found a significant correlation between the increase of thresholds in Di and MD viewing configurations ($r = 0.660$, $P = 0.038$).
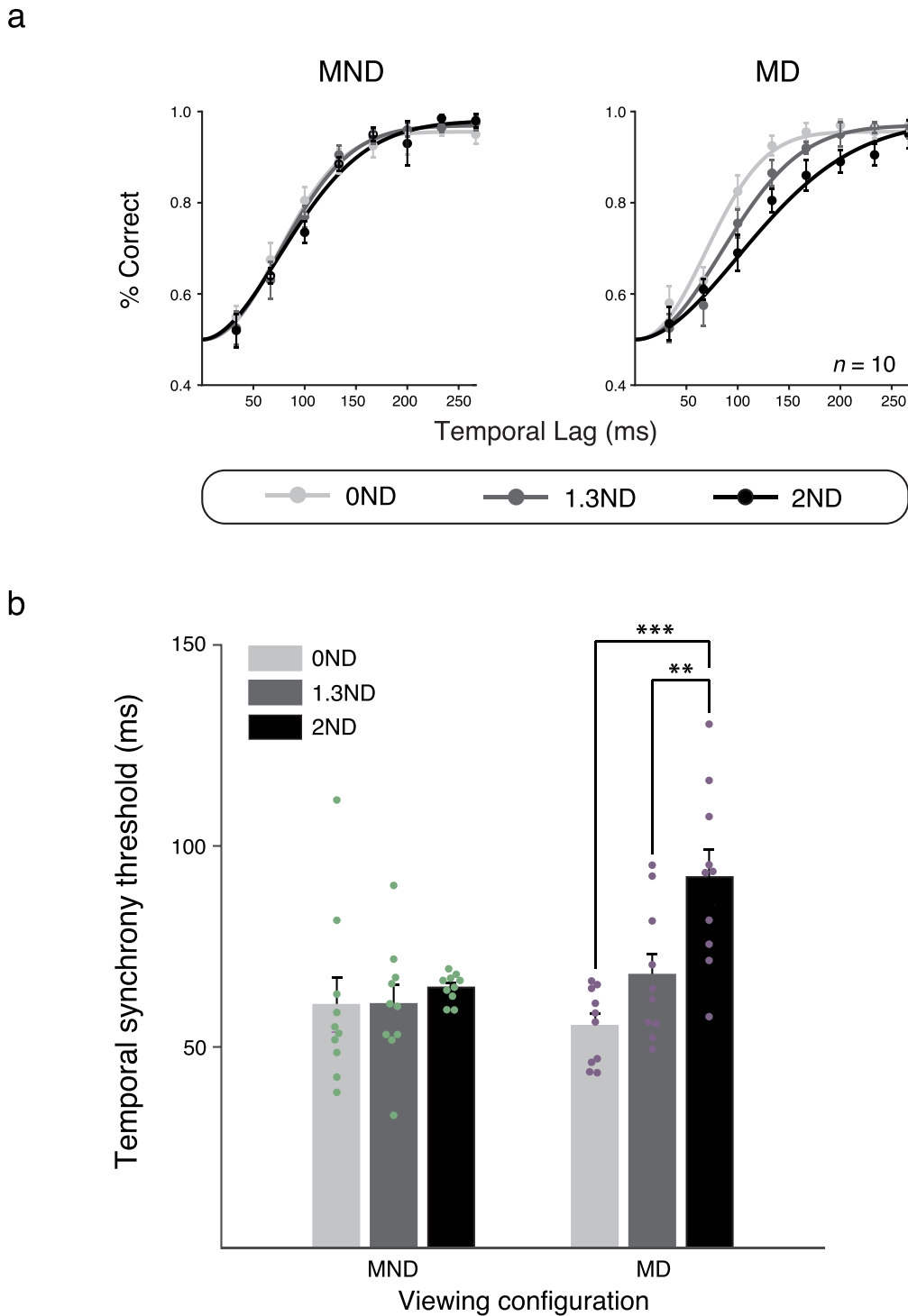
FIGURE 3. Monocular configurations results. (**a**) Mean psychometric functions. The proportion correct of all responses is plotted against the temporal lag. The different *shadse of grey* represent each luminance condition (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). The psychometric functions were fitted with Palamedes 1.8.1.[43] (**b**) Mean monocular thresholds across observers. The temporal synchrony threshold under different configurations is plotted. The different *shades of grey* represent each luminance condition (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). Each solid circle represents the monocular threshold of one observer. Error bars represent the standard errors. ** $P < 0.01$; *** $P < 0.001$.

DISCUSSION

In this study, we investigated the role of monocular luminance reduction on monocular and interocular tempo-

ral synchrony processing in human adults. Three experiments were conducted: dichoptic (experiment 1), monocular (experiment 2), and binocular (experiment 3) viewing configurations.
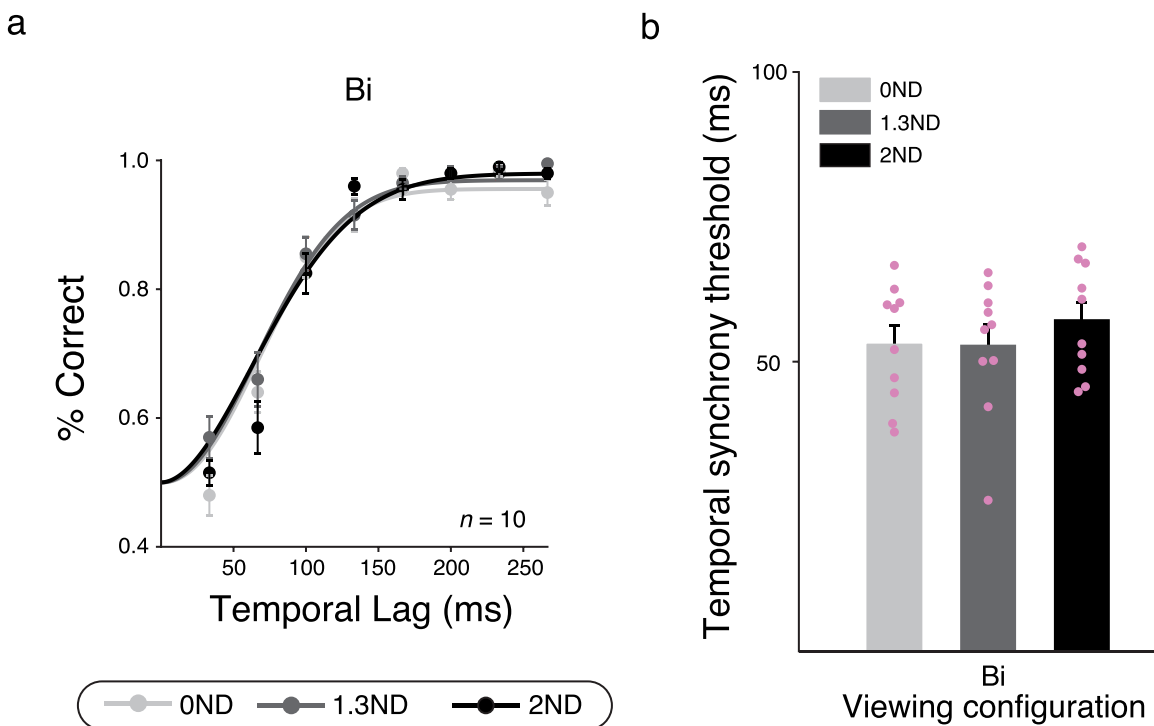
a

b

FIGURE 4. Binocular configurations results. (**a**) Mean psychometric functions. The proportion correct of all responses is plotted against the temporal lag. The different *shades of grey* represent each luminance condition (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). The psychometric functions were fitted with Palamedes 1.8.1.[43] (**b**) Mean binocular thresholds across observers. The different *shades of grey* represent each luminance condition (*black*, *dark grey*, and *light grey* for 2 ND, 1.3 ND, and 0 ND, respectively). Each solid circle represents the binocular threshold of one observer. Error bars represent the standard errors.
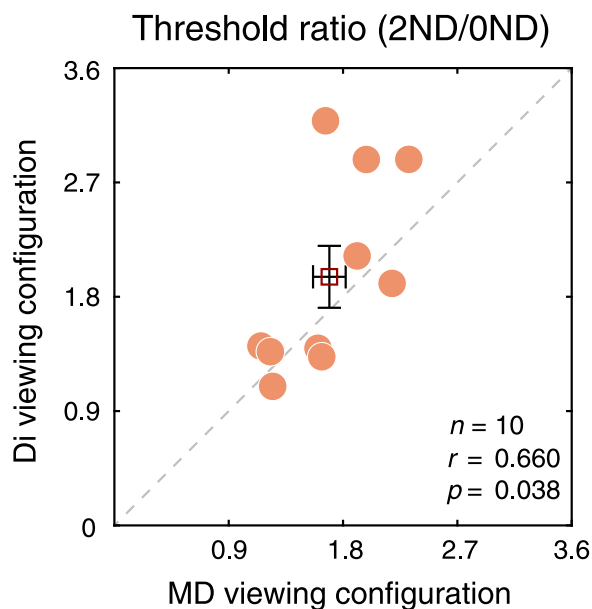

FIGURE 5. The effect of reduced monocular luminance under the Di viewing configuration as a function of effect under the MD viewing configuration. The effect of reduced monocular luminance was quantified by the threshold ratio between the 2 ND and 0 ND conditions. Each *orange dot* represents the result of one participant. The *red square* represents the average results of all participants. Error bars represent standard errors.

In experiment 1, we examined whether our paradigm works properly in the presence of interocular luminance difference by completing three configurations (D2ND, D2D, and Di). Reduced luminance has been shown to increase latency in the filtered eye,[24,25,31] thereby inducing interocular asynchrony. Under both the D2ND and D2D configurations, the threshold for temporal synchrony discrimination remained unchanged as the density of the ND filter increased. In these configurations, the signal pair was presented to one eye, be it the filtered (i.e. dominant) or unfiltered (nondominant) eye, and reference pair to the other eye. Our findings of the unchanged thresholds suggest that poorer visibility of either the signal pair or the reference pair from reduced luminance condition, per se, did not affect the threshold for temporal synchrony discrimination. However, under the Di configuration, the filtered eye of the observers perceived only one dot from the signal and reference pairs rather than a complete pair of either the reference or signal. If we were to follow the line of reasoning that interocular luminance difference increases latency in the filtered eye, the reference pair (i.e. synchronous) would appear to flicker asynchronously. This would hinder task performance and an increase in thresholds. Indeed, we observed an increase in the dichoptic threshold in Di configuration when a 2 ND filter was introduced to the dominant eye. Therefore, the premise on how reduced luminance increases visual latency in one eye seems apt to describe our findings on the elevated dichoptic threshold in Di configuration.

On the other hand, our results from experiment 2 show that reduced luminance in the filtered eye increases the monocular threshold for temporal synchrony discrimination

when both the signal and reference pairs were presented to the filtered eye only (MD configuration). In this configuration, the monocular threshold is a measure of the ability of one eye, rather than both eyes, to process and discriminate temporal synchrony in our stimulus. This configuration from experiment 2 (i.e. MD) was unique from D2ND or D2D configurations because it did not enable the subjects to use their unfiltered eye to perform the task. We found that the threshold increased in MD configuration but not in D2ND and D2D configurations. It is well known that reduced luminance increases the response latency[24,25] and amplitude[25–27] of the filtered eye. However, both mechanisms would not selectively affect the signal pair. Thus, we do not believe these mechanisms can explain our results. Instead, a separate phenomenon or mechanism that might be pertinent to temporal synchrony discrimination could explain how reduced luminance could disrupt the monocular ability to discriminate asynchronous stimuli from the synchronous ones.

In experiment 3, both the signal and reference pairs were presented to both eyes. The binocular threshold for temporal synchrony discrimination did not change even in the presence of interocular luminance difference. From our results in experiment 2, we anticipated an increase in the binocular threshold. If inputs from both eyes were weighed equally, the binocular temporal synchrony threshold in the presence of interocular luminance difference would have changed. However, it seems that the binocular temporal synchrony threshold is comparable when an ND filter is introduced or absent. This indicates that there was an inhibitory binocular interaction, in which the unfiltered eye suppressed the input from the filtered eye. This agrees with the results from Richard et al.[44] Using MEG, Richard et al.[44] recorded steady-state visually evoked potentials (SSVEPs) and observed that the magnitude of binocular SSVEPs (during which the dominant eye was filtered) was comparable to that of monocular SSVEP from the unfiltered eye. They concluded that the monocular change of response latency in reduced luminance is suppressed by the unfiltered eye in binocular viewing. Even our study focused on the response asynchrony and Richard et al.[44] focused on the response latency, the similar monocular-binocular differences in these two studies indicate that the two temporal effects (i.e. response latency and response asynchrony), might be homogeneously affected by reduced luminance before binocular combination. To confirm our speculation, we computed the correlation between the increased threshold in dichoptic viewing configuration (showing the effect of response latency) and that in monocular viewing configuration (showing the effect of response asynchrony) at low luminance (see Fig. 5). A strong correlation was found. It is likely that the changes of response latency and response asynchrony by luminance reduction reflect two different aspects of the neuronal modulation at a similar neural site.

Similar to our previous study[38] using a similar synchrony paradigm, we assumed that the psychometric slopes were equal (i.e. reduced fitting model) in the six viewing configurations (i.e. Bi, MND, MD, D2ND, D2D, and Di) for each luminance condition (i.e. 0 ND, 1.3 ND, and 2 ND). This is because a model comparison using the F-test indicated that the reduced (same slopes across all configurations) and full models (different slopes across all configurations) were statistically equivalent. The statistical equivalence indicates that the reduced model provides an adequate fit to our data in the form of a psychometric function, despite the assumption that the slopes across all configurations are equal rather than distinct. Actually, even if we had analyzed our results based on the fitted thresholds from the full model, we would still get similar thresholds and, hence, findings (i.e. temporal synchrony threshold increased only under MD and Di configurations with reduced luminance) as those in the paper. The results of the temporal synchrony threshold agree with our prediction (see Introduction) in that the increased latency in the filtered eye (i.e. the reduced luminance in one eye produced interocular delay) produces an increased temporal synchrony threshold under pure dichoptic viewing configuration. In addition, the elevated monocular threshold when the stimuli were presented in the filtered eye could be attributed to a novel mechanism rather than the presence of the increased latency or the reduced amplitude from low luminance.

Based on the reduced fitting model, the averaged slope was 2.43 ± 0.28 (average $\pm$ standard error) under 0 ND luminance condition, 2.26 ± 0.19 under 1.3 ND, and 2.13 ± 0.15 under 2 ND. These values could be the reason that the slopes of the curves in Figures 2 and 3 (the fits on average data) appear to be different. However, the ANOVA test showed that the fitted slopes at the three luminance conditions were not significantly different ($F_{2,27} = 0.48$, $P = 0.622$). Again, this was true even if a full fitting model was used to get the slopes of the psychometric functions. We, however, do not have a good explanation for the little-to-no change in slopes under different luminance conditions.

One might argue that the two neighboring dots, which were flickered at a different phase, could produce a w-motion percept.[45,46] In the presence of w-motion percept, subjects would perceive the two signal dots as a single entity in motion, moving from the disappear dot to the appear dot as if there were a proper temporal lag.[47] This perceived movement would reduce visual latency under low luminance condition,[46,48] and might affect our measurement of the temporal threshold for synchrony discrimination. We believe that w-motion could have been induced in some frames of the screen when the contrast of one signal dot was identical with that of the grey background during our psychophysical experiment. However, in most frames, the observers perceived two signal dots because there were 60 frames in one temporal cycle. It was hard for the participants to have a consistent w-motion percept throughout the task. Furthermore, we added contrast jitter on the two pair dots so that the participants observed different stimuli in different trials even when the same temporal lag condition was tested, thereby lowering the possibility of producing a w-motion percept. In addition, subjects did not report that they had perceived a motion that could occur as a result of w-motion percept throughout the task. It seems that w-motion had a very little effect on the task performance of our subjects. Nevertheless, the multiple visual latencies produced by w-motion, even if occurred, might only affect the temporal synchrony threshold measurement under dichoptic, not monocular, viewing configuration. As it is discussed previously in the paper, the increased monocular threshold for temporal synchrony cannot be explained by the fact that reduced luminance increases visual latency. We thus believe that our main conclusion is unaffected from multiple visual latencies produced by w-motion.

The temporal synchronous firing of neurons are thought to be the underlying mechanism[49] for visual grouping[50,51] and figure-ground segmentation.[35–37] When neurons

are activated by a coherent stimulus, they would fire synchronously (i.e. visual grouping).[52–54] On the other hand, when activated in an asynchronous fashion, the neurons would fire in a unit of subpopulation and be distinguished by the temporal coherence of the asynchronous activity (i.e. visual segmentation).[53,54] This synchronization has been considered to be based on a selective network of corticocortical and corticothalamic connections.[49,55] The abnormalities of connections linking neurons have been suggested to be the reason for reduced synchronization in amblyopic eyes.[56] The abnormal temporal synchrony in patients with amblyopia also has been observed recently by Tao et al.[38] It is probable that neuronal connections might be disrupted at reduced luminance, thereby manifesting an increase in the threshold for temporal synchrony discrimination.

The clinical relevance of interocular luminance difference to monocular and interocular asynchrony is evident. There have already been numerous reports on how patients with medical conditions, such as unilateral cataract[12,13] and traumatic anisocoria,[15] show naturally occurring interocular difference in retinal illuminance. These patients would show poor binocular summation, stereopsis, and monocular sensitivity for discriminating asynchrony in everyday life. Investigating the "response asynchrony" of the affected eye of patients with these medical conditions could broaden our understanding of these eye diseases. Furthermore, it would be interesting to test whether we can treat these visual deficits by reducing luminance of the unaffected eye, as it has been demonstrated by Zhou et al.[8] and Ding et al.[19] in a population of adults with amblyopia.

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