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A brief light reduction induces a significant delay in the previously dimmed eye

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Abstract

Purpose: We investigated how a short-term luminance reduction in one eye can influence temporal processing of that eye after luminance is restored by measuring the relative delay between the eyes.

Methods: A paradigm based on the Pulfrich effect, which is a visual illusion of depth when no depth cue is present, was used to measure relative delay in visual processing between the eyes. We deprived the monocular luminance in adults with normal vision across different intensities. In the first experiment, the ratio of the light level between the eyes stayed constant, whereas the absolute value was allowed to vary. In the second experiment, both the ratio and the absolute light level stayed constant, by controlling the environmental light level. In both experiments, we measured the changes in relative delay before and after 60 min of light deprivation.

Results: Our results indicated that short-term monocular deprivation of luminance slows the processing in the previously dimmed eye and that the magnitude of the delay is correlated with the degree of luminance reduction. In addition, we observed that the absolute luminance difference, rather than the absolute luminance levels seen by the dimmed eye, is important in determining the magnitude of delay in the previously dimmed eye. These findings differ from what has been reported previously for the monocular deprivation of contrast.

Conclusions: Taken together, these findings support the view that short-term deprivation of visual information could affect two distinct mechanisms (contrast gain and temporal dynamics) of neural plasticity.

KEYWORDS
binocular vision, interocular delay, luminance, Pulfrich effect, stereopsis

INTRODUCTION

The visual system can function across an impressive range of luminance differences. However, the luminance level between the eyes has to be equal for optimal visual processing. Otherwise, binocular balance,[1] interocular temporal synchrony[2] and depth perception[3] are compromised. For example, the difference in the interocular light level can induce the Pulfrich effect, which is a century-old illusion of depth in the absence of disparity.[4] The dimmed eye processes visual information more slowly as the speed of neural conduction/processing is decreased.[5] The Pulfrich effect causes a sensation of depth when an observer with an interocular luminance imbalance is viewing a pendulum that is swinging horizontally from left to right, resulting in an illusion of motion-in-depth. The Pulfrich effect can also be demonstrated in visually impaired individuals due to anatomical or neural pathologies that produce interocular imbalances. For example, unilateral cataract reduces the light transmission through the affected crystalline lens.[6] Furthermore, amblyopia, a cortical pathology that affects the processing of the input from one eye, exhibits differences in processing speed between the eyes.[7–9]

Clinical studies show that the placement of neutral density or tinted filters before the unaffected eye for months can abolish the Pulfrich effect for years in visually impaired adults.[10,11] This supports the notion that the adult visual cortex has residual neural plasticity where spatiotemporal information is concerned,[12,13] and that temporary luminance deprivation can induce a more prolonged delay in visual processing beyond the deprivation period. For example, occlusion of one eye for a short period of time (15 min to 5 h) results in a change in ocular dominance that lasts for up to an hour.[14–16] Primate studies show that these perceptual changes in eye dominance are correlated with physiological changes in ocular dominance columns in the primary visual cortex.[17,18] Moreover, human electrophysiology studies suggest that these ocular dominance changes as a result of short-term monocular occlusion are reciprocal in nature: the contrast gain of the previously patched eye is increased and that of the previously unpatched eye reduced.[19,20]

A change in the mean light level between the eyes would be expected to also change the contrast gain of visual processing,[21] and shift eye balance in a way that is comparable to monocular occlusion. The expectation based on what we know from the monocular deprivation literature is that these contrast gain-based effects depend on the interocular luminance ratio, namely, the relative light levels in the two eyes. However, Yao et al. showed that the absolute, not the relative difference in the light level, determines the shift in eye balance.[22] Their findings indicate that the changes in eye-balance that occur from the deprivation in mean luminance of one eye may involve changes in contrast gain at both retinal and cortical sites.

Recently, whether functional plasticity of perceptual balance and temporal processing have a common neural basis has sparked an interest amongst researchers. For example, by measuring the Pulfrich effect after monocular deprivation, Novozhilova et al. reported that the previously deprived eye exhibited a Pulfrich effect consistent with a delay in the deprived eye.[13] This change is opposite to that expected based on the contrast gain model that describes the process of binocular combination.[14,20,23] This result suggests that the neural mechanism that governs delay and balance might differ because of monocular deprivation.

In our study, we explored whether short-term monocular luminance deprivation induces interocular delay after the deprivation and aimed to characterise the underlying mechanisms using psychophysics. We raised two questions. First, does the induced delay after luminance deprivation in one eye have a similar time decay to that from changes in binocular balance after contrast deprivation? Second, does the delay in the previously luminance-deprived eye depend on the absolute luminance seen by the deprived eye or the relative luminance difference between the eyes? The answer to these two questions bears upon whether eye balance and temporal neuroplastic changes after monocular deprivation have a common neural basis, even though one might not necessarily be a consequence of the other. To address these issues, we performed two experiments. In the first experiment, the relative difference of the light level between the eyes stayed constant, whereas the absolute light level in the deprived eye was allowed to vary. In the second experiment, both the relative light level (i.e., ratio) and absolute light level in the deprived eye stayed constant. In both experiments, we measured the changes in relative delay before and after 60 min of mean luminance deprivation to one eye.

Key points

- The difference in the light level between the eyes can induce the Pulfrich effect, which is a century-old illusion of depth in the absence of disparity.
- Monocular deprivation of luminance for 1 h causes the Pulfrich effect by delaying the previously dimmed eye, reflecting a potent after-effect.
- Both absolute and relative luminance differences between the eyes, rather than the light level seen by the dimmed eye during the deprivation, could affect the magnitude of the Pulfrich effect.

MATERIALS AND METHODS

Participants

Ten adults with normal or corrected-to-normal visual acuity participated in the study (mean age: 27 ± 5.4 years, one author, five females). Nine of the 10 adults participated in Experiment 1, and eight of the 10 adults (seven of which who also participated in the first experiment) participated in Experiment 2. This study was in accordance with the Declaration of Helsinki and was approved by the Ethics Review Board of McGill University. All subjects provided informed written consent.

Stimuli and task

An illusory rotating cylinder (i.e., motion-in-depth) was perceived during the stimulus presentation (Figure 1a,b). It was constructed from 200 Gabor elements that were

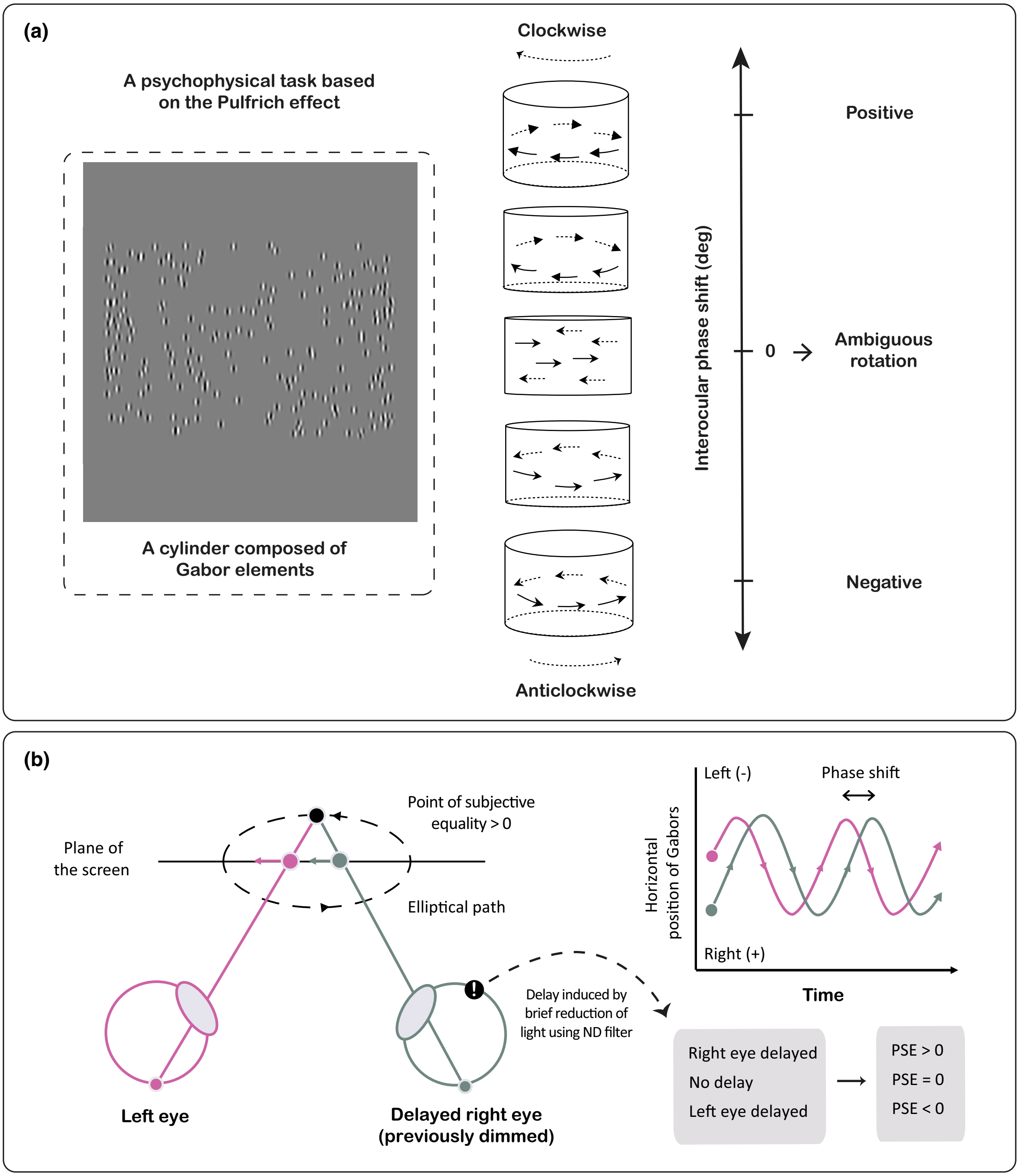

FIGURE 1 An illustration of the psychophysical task based on the Pulfrich effect. (a) Monocular stimuli as shown on the screen presented to one eye. When one eye processes more slowly than the other, this difference produces an interocular phase shift between the positions of the Gabor elements shown to each eye. Hence, the images shown to the corresponding retinal points will slightly be out of synchrony, thereby causing binocular spatial disparity. Therefore, depth perception will occur. If the interocular phase shift is negative, the direction of the perceived rotation will be anticlockwise. If it is positive, the direction of the perceived rotation will be clockwise. If it is around 0, there will be no illusory depth perception, and the direction of the rotation will be ambiguous to the observer. (b) if there is a horizontal difference between the positions of the Gabor elements shown to each eye, binocular spatial disparity will be induced. This, in turn, causes a perception of depth even if the stimuli themselves do not have depth. In the case of our study, the previously luminance-deprived right eye shows delay, thereby inducing a perception of anti-clockwise rotation (PSE > 0). If the left eye is delayed, the point of subjective equality (PSE) will be negative. If the right eye is delayed, the PSE will be positive. If there is no relative delay between the eyes, the PSE will be zero.

dichoptically displayed; the identical Gabor elements were presented to both eyes with horizontal disparity. Gabor elements were formed as a product of a sinusoidal and Gaussian function. Each Gabor element had a size of 0.15° sigma, a spatial frequency of 2.85 c/d, and a random phase. No fixation point was shown on the screen. The elements moved (i.e., oscillated) along the horizontal plane (between left and right) of the screen with a sinusoidal angular speed of 18°/s. The cylinder subtended 18° (width) × 12° (height) visual angle and was displayed for 800 ms.

An interocular phase shift (right eye relative to left eye phase) induced spatial disparity (Figure 1c) because the horizontal position of the Gabor elements between the eyes differed (see Figure 1d). Therefore, Gabor elements appeared as if they moved along an elliptical trajectory of motion in depth. If the interocular phase shift is negative, then the direction of the perceived rotation will be anticlockwise. If it is positive, the direction of the perceived rotation will be clockwise. If it is around zero, there will be no illusory depth perception, and the direction of the rotation will be ambiguous to the observer. The relative delay between the eyes was quantified with the outcome measure of the point of subjective equality (PSE) where the cylinder appears to be rotating in an ambiguous direction. By using the method of constant stimuli, we showed stimuli in every test block at many phase shifts with 10 repetitions per phase: −0.75°, −0.375°, −1.875°, −0.0938°, −0.0469°, −0.0234°, 0°, 0.0234°, 0.0469°, 0.0938°, 0.1875°, 0.375° and 0.75°.

If the left eye is delayed, the PSE will be negative because a negative PSE indicates a larger likelihood for the observer to perceive a clockwise rotation given an interocular phase shift. Hence, the observer requires less interocular phase shift for the eye to perceive the clockwise rotation of the cylinder. On the other hand, if the right eye is delayed, then the PSE will be positive because the eye is more likely to see an anticlockwise rotation of the cylinder given an interocular phase shift. Therefore, the observer will require a larger, positive interocular phase shift to perceive a clockwise rotation of the cylinder. When neither eye is delayed relatively to one another, the PSE will be 0.

The task of the observer was to report the perceived direction of the cylinder using the keyboard. The psychophysical task was a two alternative forced choice. The two responses corresponded to either clockwise or anticlockwise rotations. There was no time limit for the response.

Experimental design and rationale

To explore whether absolute or/and relative luminance difference is important for inducing delay after monocularly depriving luminance, we performed two experiments in natural or controlled viewing conditions.

Experiment 1: Luminance deprivation in a natural viewing condition (interocular luminance ratio during deprivation was constant)

Nine subjects participated in Experiment 1 in a natural viewing condition (see Figure 2). First, they completed three blocks of a baseline test that measured the Pulfrich effect, which is induced by a relative delay between the eyes, in a dimly lit experimental room. Next, luminance was deprived with a custom-made eye patch that encased an ND (neutral density)-filter, either 0- (no filter), 1-, 2- or 3-ND (100%, 10%, 1% and 0.1% light transmittance, respectively). It was placed in front of their right eye for 60 minutes. Throughout the deprivation, they were allowed to be anywhere in the building that housed the experimental room. Then, they performed post-deprivation measurements in the testing room at 0, 5, 10, 20 and 30 min after the deprivation. During this experiment, the absolute light level of the environment could vary, but the interocular luminance ratio remained constant. Hence, this experiment allowed us to examine the role of relative luminance difference between the eyes.

Experiment 2: Luminance deprivation in a light-controlled viewing condition (absolute luminance of the deprived eye was constant during deprivation)

Eight subjects (including seven of the nine subjects from Experiment 1) participated in Experiment 2 in the controlled viewing condition, during which the absolute luminance difference was constant. Subjects were asked to remain in the testing room where the light level was kept at about 10 cd/m^2 throughout the experiment (see Figure 2). During the deprivation, we dimly displayed a movie to prevent the participants from falling asleep in the dark.

Data interpretation

Two experiments were conducted in this study. The first experiment used deprivation consisting of a constant interocular luminance ratio. For instance, depending on where the observer was in the building, the absolute light level could vary. However, the ratio in the light level between the eyes stayed the same due to the ND filter in front of the right eye. Also, the ambient light in the natural viewing condition (Experiment 1) was brighter (by 10×, ~100 cd/m^2) than the controlled viewing condition (Experiment 2). In the second experiment, the overall surrounding light level was fixed at about ~10 cd/m^2 (see Figure 2), which was the overall average luminance level on the desk and walls around the subject's seat in the experiment room.

Our experimental designs could inform whether the absolute or relative luminance difference, or the absolute light level seen by the previously dimmed eye was important in inducing the Pulfrich effect (i.e., interocular delay). Here are four possible scenarios.

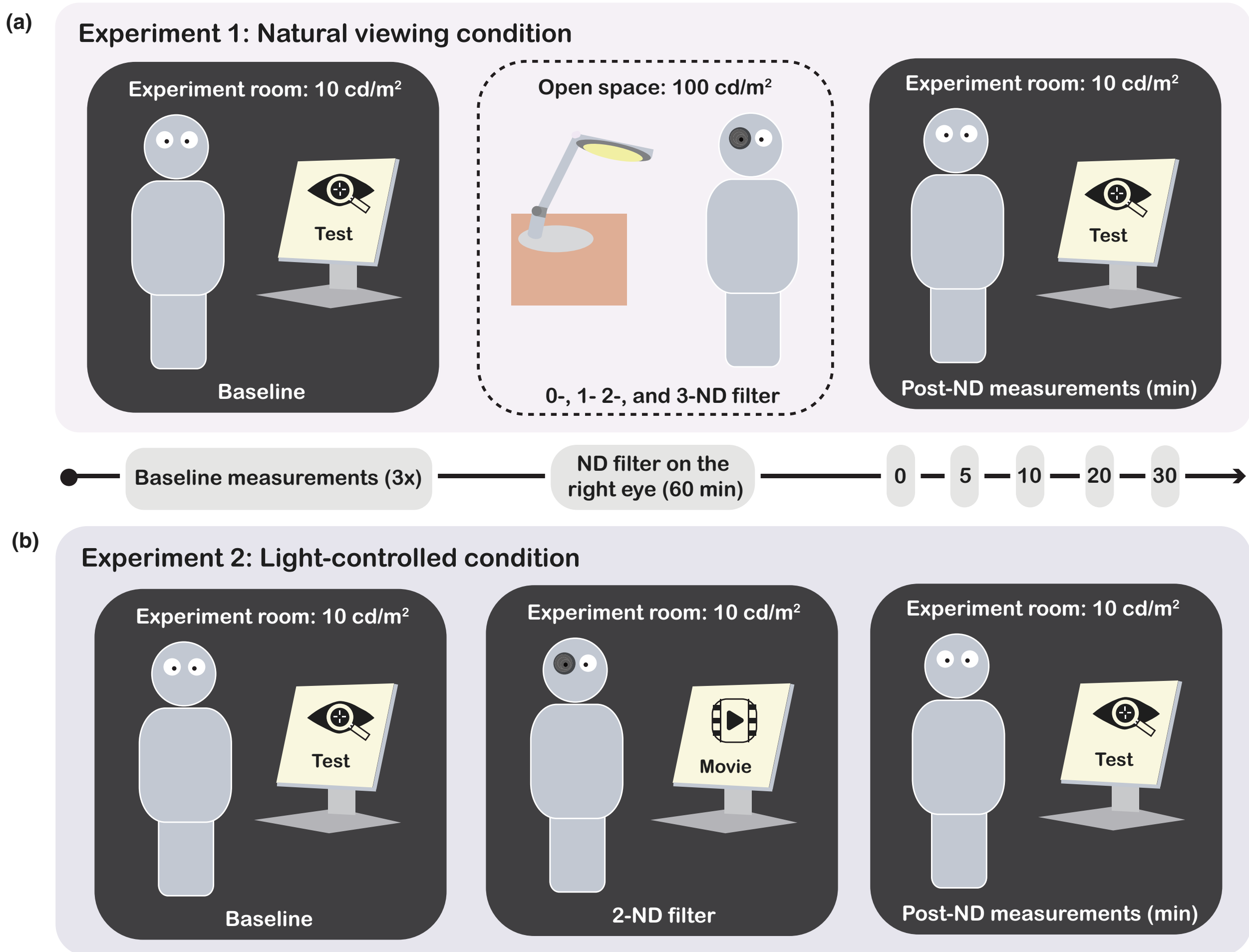

FIGURE 2 The protocol of our design. (a) Illustration of experiment 1 in a natural viewing condition. Subjects were asked to perform three repetitions of baseline measurements before undergoing monocular luminance deprivation for 60 min using either a 0-, 1-, 2-, or 3-neutral density (ND) filter. Then, they performed the same measurement at 0, 5, 10, 20 and 30 min after the luminance deprivation period. They could stay anywhere in the laboratory space (i.e., outside the experiment room, where the luminance level was approximately 100 cd/m^2 during the deprivation period. (b) Illustration of experiment 2 in a controlled viewing condition. Subjects were asked to perform three repetitions of baseline measurement before undergoing luminance deprivation for 60 minutes using 2-ND filter (factor of 100 reduction) during which they were asked to stay in the experiment room (luminance level ~10 cd/m^2) so that the surrounding level would be controlled. Then, they performed the same experiment at 0, 5, 10, 20 and 30 min after the luminance deprivation.

If only the absolute luminance difference mattered, then the observer would experience a significantly longer delay under the natural viewing condition than under the controlled condition from wearing the same ND filter (for example, 2-ND in Experiment 2). In addition to this hypothetical scenario, if the relative luminance difference did not induce the delay, the previously dimmed eye would not experience a significant delay.

In addition, if only the relative luminance difference mattered, then the delays could also be similar in their magnitude as long as the interocular luminance ratios were similar between the natural and uncontrolled viewing conditions. For instance, if there was no difference in delay between the natural (absolute luminance difference: 99 cd/m^2) and controlled viewing experiments (absolute luminance difference: 9.9 cd/m^2) during Experiment 2 (using 2-ND in both viewing conditions), but each of them showed a delay that was significantly different from zero, then the relative difference in luminance could drive the delay.

If both the absolute and relative luminance differences mattered, there could be two ensuing scenarios. First, if the observer's previously dimmed eye underwent a delay that was significantly larger in the natural viewing condition than in the controlled condition while wearing the same ND filter (for example, 2-ND in Experiment 2), the absolute luminance difference would matter. Second, the controlled viewing condition would induce a significant delay in the previously dimmed eye, thereby indicating that the relative luminance difference mattered.

Lastly, whether the absolute light level seen by the previously dimmed eye mattered could be resolved by comparing the results between Experiment 1 (3-ND filter) and Experiment 2 (2-ND filter) because the light seen by the dimmed eye would be approximately the same (~0.1 cd/m^2). If the light level seen by the deprived eye determined the magnitude of the delay, delays of similar magnitudes in the previously deprived eye could be induced between the natural (3-ND) and controlled (2-ND) viewing conditions. Instead, if they were significantly different, however, then the interocular difference in luminance could be important in inducing the delay rather the absolute light level seen by the dimmed eye.

Apparatus

The experiment was programmed using MATLAB 2015a (MathWorks, mathworks.com) with the Psychtoolbox extension 3.0.8 (Psychophysics Toolbox Version 3, psychtoolbox.org). It was performed on an Apple MacPro computer (apple.com) with a Linux Mint (linuxmint.com) operating system and a Nvidia GeForce GT graphics card (nvidia.com). Stimuli were presented separately (i.e., dichoptically) to each eye on a wide 23-inch-3D-Ready LED monitor ViewSonic V3D231 (viewsonic.com). The gamma-corrected screen had a mean luminance of 100 cd/m^2, a resolution of 1920 × 1080 pixels, and a refresh rate of 60 Hz in interleaved lines stereo mode. In a dimly lit room, subjects completed the experiment at 90 cm from the screen and wore polarised 3D glasses, which reduced the luminance by 60% and induced a crosstalk of 1%.

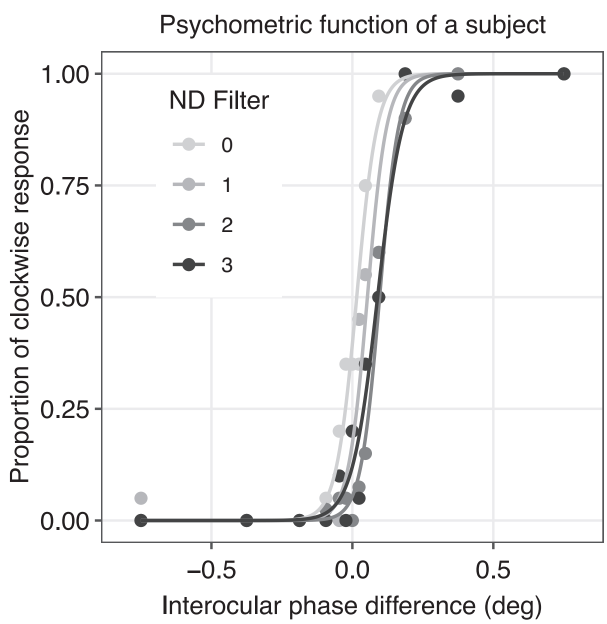

FIGURE 3 Psychometric functions of a representative subject after 60 minutes of monocular luminance deprivation with a zero, 1-, 2- or 3- ND filter in the natural viewing condition (experiment 1). The abscissa represents the interocular phase difference (°), whereas the ordinate denotes the proportion of clockwise response from the observer. A logistic function was used to fit the psychometric functions. By using the fits, we were able to estimate the interocular phase difference where the proportion of clockwise response was at 50%. This point is referred to as the point of subjective equality (PSE) because both the clockwise and counter clockwise rotations are seen at the same rate (i.e., ambiguous rotation of the cylinder). The PSE (°) seems to increase as the neutral density (ND) filter gets denser, as illustrated by the fact that the darker curves are shifted to the right along the x-axis.

Data analysis

The PSE in degrees was defined as the interocular phase shift where a subject sees the cylinder rotating clockwise 50% of the time. Psychometric functions were reported as the proportion of clockwise perception in the function of interocular phase shift (Figure 3). They were fitted with logistic functions, from which the PSE was estimated. If the PSE was negative, then the left eye was delayed more; if the PSE was positive, the right eye was delayed more. To compute the effect driven by ND filters, we calculated the changes in PSE after the deprivation relative to baseline (PSE after deprivation – PSE before deprivation). These computations were performed in MATLAB 2015a.

We performed a two-way, repeated measures analysis of variance (ANOVA) by designating time after deprivation and ND type as within-subject factors. This was completed using the rstatix package in R software (The R Project, cran.r-project.org).[24] In addition, we performed a random-effects analysis using the lmerTest package[25] to assess whether the associated effects changed the means of Δ PSE shift after luminance deprivation. To obtain the most parsimonious model, we performed a likelihood ratio test using ‘anova()’ in R software[26] as a nested model comparison.

RESULTS

Experiment 1: Luminance deprivation in natural viewing condition

A representative subject's psychometric functions from Experiment 1 are shown in Figure 3. This is averaged data from two time points after the period of deprivation (0 and 5 minutes) per condition. Each plot shows a different condition in Experiment 1. When the ND filter increasingly blocks the light transmission (i.e., darker plots), the psychometric function shifts to the right. This indicates that as the ND filter increasingly reduces light transmission in the right eye for the period of deprivation, the PSE becomes more positive after deprivation, indicating that the right eye is more delayed.

Figure 4 presents the difference in PSE between baseline and post-deprivation (Δ PSE shift). A positive Δ PSE shift indicates a larger relative delay in the deprived eye (i.e., right) than in the other eye. Each shade of the plot (from light grey to black) indicates ND filter intensity. There is no change in the control 0-ND condition. Otherwise, we can see that the stronger the filter, the larger the Δ PSE shift. The changes in PSE shift at 0 minute after the deprivation using 1-ND filters is about 0.015 degrees, whereas the shifts from 2- and 3-ND filters are about 0.03 degrees. A positive Δ PSE shift of 0.03 degrees is equivalent to a 1.65 ms delay in the deprived eye compared to the non-deprived eye. The changes in the PSE shift fade within 5–10 min. To determine whether the delay differed significantly amongst the conditions, we performed a 2-factor repeated measure ANOVA by considering the effect of the ND filter type and the time points as the fixed effects. We decided to perform this analysis by including the factors as fixed effects based on the definition by Gelman.[27] The analysis revealed no significant effect of ND filter type (F (3, 24) = 2.28, p = 0.11) and a significant effect of time after patching (F (4, 32) = 4.98, p = 0.003). The interaction between ND filter type and time point was also significant (F (12, 96) = 3.44, p < 0.001), indicating that the decay of the Δ PSE shift over time plots differed significantly amongst the four experimental sessions with unique ND filters.

In addition, we performed a random-effects analysis by treating the factors as random effects, from which we estimated three sources of variance: (1) variance between the subjects, (2) variance between the type of the ND filter and the subjects and (3) variance between the time points and the subjects. The likelihood ratio test, which was used to perform a nested model comparison, revealed that inclusion of the variance between the subjects, as well as the variance between the ND filter and the subjects, better described the data. By applying the Satterthwaite approximation for the degrees of freedom, we computed the statistical significance of the three random effects (i.e., p-values). We observed that the random effects of subjects and between the ND type and subjects were statistically significant (p < 0.05) but not the random effect that accounts for the variance between the time points and the subjects.

Δ PSE shift did not significantly differ from zero at 10, 20, and 30 min (p > 0.05, one-sample t-test) after patching

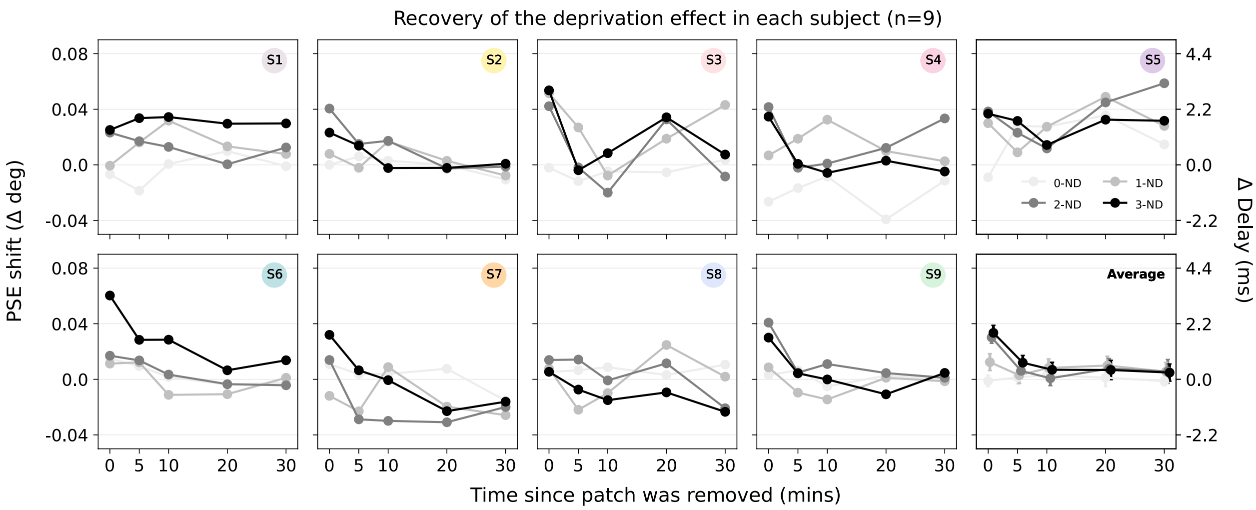

FIGURE 4 Effects of monocular light deprivation averaged from nine observers under the natural viewing condition in experiment 1. These data show individual and averaged changes of the point of subjective equality (PSE) shift (relative to baseline data) across the observers at all time points from 0 to 30 min after deprivation. Each shade of grey represents deprivation with a different neutral density (ND) filter: 0 (no filter), 1, 2, or 3 ND from light to dark grey.

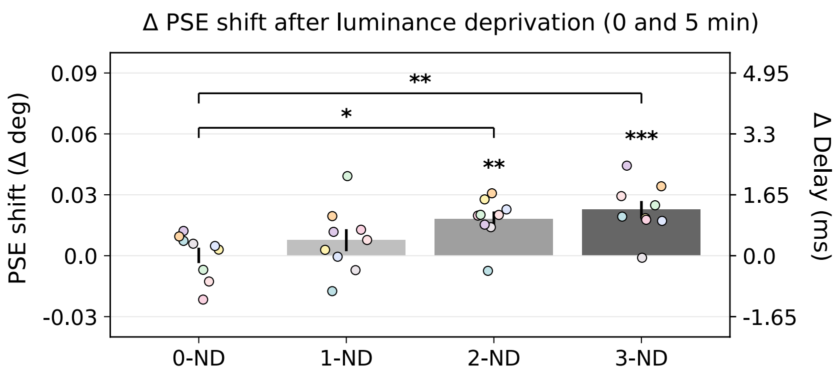

FIGURE 5 Averaged immediate changes in the point of subjective equality (PSE) shift after monocular luminance deprivation (relative to baseline data). These are the mean of the data from 0 and 5 min after the deprivation. Each dot with unique colour represents each subject (same colours as Figure 4). Asterisks on top of the bar denote statistical significance from 0 (i.e., one-sample t-test), such that $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Asterisks on top of the bridge show statistical significance from pairwise comparisons (pairwise t-tests between two natural density (ND) conditions).

for most conditions. To better illustrate the immediate effect of monocular luminance deprivation for each ND filter, we averaged the Δ PSE shift effect across the 0–5 min after patching (see Figure 5). The averaged Δ PSEs from 0 to 5 min were significantly different from zero for 2- and 3-ND filters (one-sample t-test, $p < 0.01$) but not so with 0- and 1-ND filters. We can clearly see the trend that the stronger the filter, the larger the induced delay.

Experiment 2: Luminance deprivation in a light-controlled condition

To examine whether the deprivation of absolute and/or relative luminance was important in driving an interocular delay after deprivation, we performed a second experiment in controlled lighting. Participants had to remain in the experimental room that had a low level of ambient illumination (~10 cd/m^2, a factor of 10 lower than for Experiment 1) throughout the entire experiment, including during the deprivation. As opposed to the first experiment, Experiment 2 allowed us to compare the effect of deprivation for an interocular luminance difference where the absolute luminance levels were held constant during the period of deprivation. The results are shown in Figure 6, which displays the effect of a 2-ND filter deprivation (a factor of 100 relative interocular luminance) in two conditions, one where the absolute luminance was a factor of 10 higher (Experiment 1) than the other (Experiment 2). The natural viewing condition (data from Experiment 1) is shown in grey, whereas the light-controlled condition is shown in purple (Figure 6). To investigate whether the magnitude of the Δ PSE shift differed between luminance deprivation in natural and light-controlled conditions, we performed a two-factor repeated measures ANOVA, which revealed a significant effect of viewing condition ($F(1, 7) = 14.39$, $p = 0.007$) and a significant effect of time after patching ($F(4, 28) = 5.16$, $p = 0.003$). The interaction between the viewing condition and time point was not significant ($F(4, 28) = 2.38$, $p = 0.12$), suggesting that the time courses of the delay decaying over time (see Figure 6) were not significantly different between the natural and light-controlled viewing conditions.

In light of our results, the absolute light level seen by the deprived eye with a 3-ND filter in a natural viewing

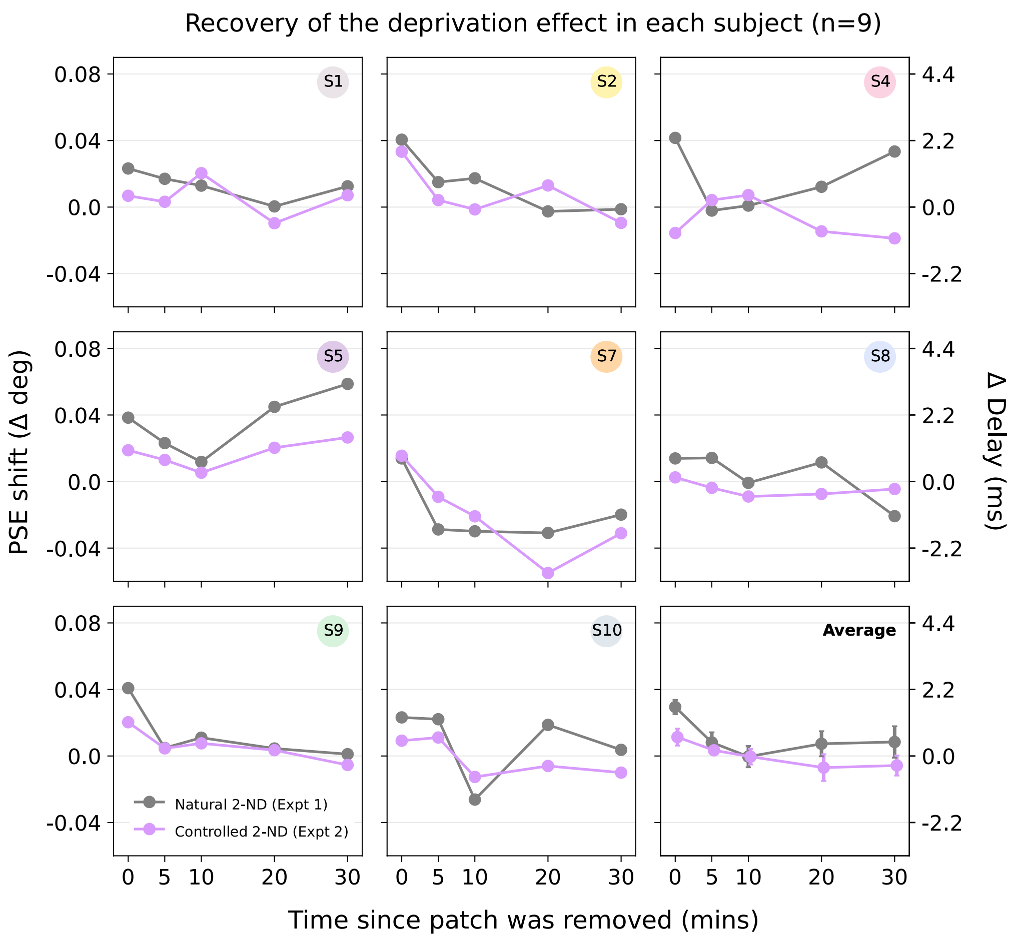

FIGURE 6 Effects of monocular light deprivation from eight observers under the natural viewing condition and light-controlled viewing condition in experiment 2. These data show individual and averaged changes of the point of subjective equality (PSE) shift (relative to baseline) across observers at all time points from 0 to 30 min after deprivation using a 2- neutral density (ND) filter in a natural viewing condition (grey) or reduced-light controlled condition (purple).

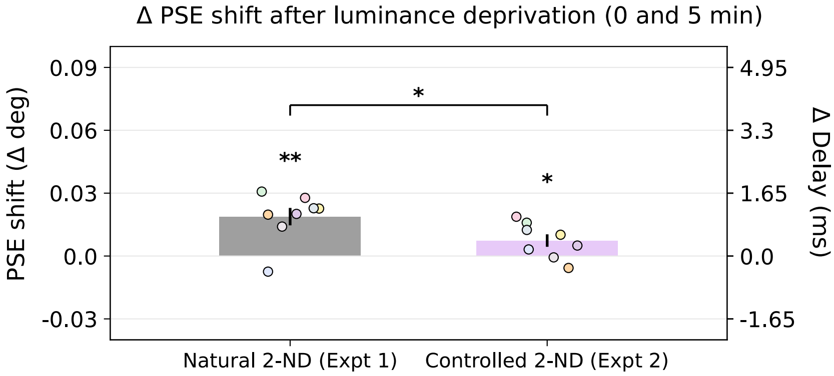

FIGURE 7 Averaged immediate changes in the point of subjective equality (PSE) shift after luminance deprivation (relative to baseline data). The grey bar represents experiment 1 (natural viewing condition); the purple bar represents experiment 2 (controlled viewing condition). They both denote the means of the data from 0 and 5 min after the deprivation. Each dot with unique colour represents each subject. Asterisks on top of the bar denote statistical significance from 0 (i.e., one-sample *t*-test), such that *$p < 0.05$, **$p < 0.01$. Asterisks on top of the bridge show statistical significance from pairwise comparisons (pairwise *t*-tests between two ND conditions).

condition (Experiment 1; Figure 4) and with a 2-ND filter in a light-controlled condition (Experiment 2; Figure 6) were similar (~0.1 cd/m^2). However, the 3-ND filter in the natural viewing condition induced a significantly longer delay than 2-ND in the light-controlled condition (1.27 ms vs. 0.41 ms; unpaired *t*-test: $p < 0.05$). These findings suggest that it is the interocular luminance difference, rather than the absolute luminance seen by the deprived eye, that determines the magnitude of the Pulfrich effect.

Furthermore, we performed a random-effects analysis. We estimated three variances as before, namely: (1) variance between the subjects, (2) variance between the type of the ND filter and the subjects and (3) variance between the time points and the subjects. The likelihood ratio test showed that the variance between the subjects could describe the data without the need for the other two sources of variance.

Since the Δ PSE shift at 10, 20 and 30 min did not differ significantly from zero ($p > 0.05$, one-sample *t*-test), we decided to do a separate analysis only for the more immediate Δ PSE shifts by averaging the Δ PSE shift from 0 and 5 min (Figure 7). These delays were significantly different from zero for the two conditions (one-sample *t*-test, controlled viewing $p = 0.04$; natural viewing $p = 0.007$). This result indicates that the relative difference in luminance can drive a significant delay in the deprived eye. However, it also seems that the absolute difference in luminance can significantly *potentiate* the magnitude of delay in the deprived eye because the natural viewing condition, which has a larger absolute difference in the light level between the two eyes, caused a much longer delay in the deprived eye than in the light-controlled condition.

DISCUSSION

These results, especially from Experiment 2, demonstrate that absolute and relative differences in luminance are both important in inducing interocular delay in the previously deprived eye. Experiment 2 indicates that the delay induced by a 2-ND filter under natural viewing conditions was significantly longer than that from the light-controlled condition; this result illustrates that the absolute luminance difference is important in inducing the delay. In addition, the delay induced under the controlled viewing condition was significant even if there was a difference in absolute luminance of only 9.9 cd/m^2 between the eyes in this viewing condition. Conversely, we did not observe a significant peak delay (mean of delay at 0 and 5 min after the deprivation) in the natural viewing condition after the eye was deprived with the 1-ND filter; there was a difference in absolute luminance of about 90 cd/m^2, thereby indicating that the relative luminance difference could be important in inducing the delay. Furthermore, even if the absolute light level seen by the dimmed eye was similar between the natural (3-ND filter) and controlled (2-ND) viewing conditions, the delay was significant only for the latter condition. These findings show that both the absolute and relative luminance differences induce the Pulfrich effect.

Our findings bear upon the relationship between the changes in eye balance and temporal-based changes that influence the Pulfrich effect after one eye's light level has been deprived for a short period. It would seem that these two visual effects resulting from the same type of deprivation reflect different neural mechanisms. First, the eye-based changes that are thought to reflect shifts in the contrast gain of the visual system predict a temporal after-effect in the opposite direction to that observed with the Pulfrich effect,[13] namely, a speeding up of the previously deprived eye because of its increased contrast gain. Second, the time course of the eye-balance and temporal after-effects are quite different, with the former being about 3–6 times slower.[14,15,20] Third, while there is a role that luminance deprivation per se might play in the eye-balance after-effect,[22] we found that the temporal after-effect is driven by the absolute and relative differences in luminance between the eyes. Taken together, these findings support the view that the neuroplastic changes that occur because of short-term deprivation of visual information (which can reduce both the contrast and overall luminance) could result in two different after-effects, one involving contrast gain that affects eye balance and the other involving luminance, each subserved by a separate, binocular neural mechanism.

The Pulfrich effect can disturb motion perception and impact real-world tasks such as driving[28–30] and sports performance.[31,32] Unfortunately, it is often ignored in the clinic since the symptoms can be complex and puzzling for both clinicians and patients.[33] A case study suggests that placing a neutral density filter longitudinally abolishes a naturally occurring Pulfrich effect in individuals with severe delay in one eye for up to 3 years.[34] Here, we show that normal adults experience only a brief, but significant, delay (for 10 min) after short-term deprivation of the luminance to one eye. It is possible that repeated rounds of luminance deprivation could induce a long-lasting perceptual change in temporal processing speed in the previously dimmed eye. Future studies should explore the clinical potential of luminance deprivation in relieving the naturally occurring Pulfrich effect in individuals with anatomical or neural abnormalities that create a mismatch in the speed of visual processing between the eyes.

CONCLUSION

In this study, the Pulfrich effect was examined in normally sighted observers who were deprived of luminance in one eye for 60 minutes. We show that absolute and relative luminance differences are important in producing a significant delay in the previously dimmed eye, thereby inducing the Pulfrich effect. We also show that this temporal after-effect is not as long lasting as its contrast-based counterpart that affects eye balance. Both findings support the view that the contrast-based, eye balance and temporal-based after-effects from short-term monocular deprivation may reflect distinct neural mechanisms.

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AUTHOR CONTRIBUTIONS

Seung Hyun Min: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); software (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Alexandre Reynaud:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); software (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal). **Robert F. Hess:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

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