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The duration effect of short-term monocular deprivation measured by binocular rivalry and binocular combination

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ABSTRACT

The ocular dominance shift observed after short-term monocular deprivation is a widely used measure of visual homeostatic plasticity in adult humans. Binocular rivalry and binocular combination techniques are used interchangeably to characterize homeostatic plasticity, sometimes leading to contradictory results. Here we directly compare the effect of short-term monocular deprivation on ocular dominance measured by either binocular rivalry or binocular combination and its dependence on the duration of deprivation (15 or 120 min) in the same group of participants. Our results show that both binocular rivalry and binocular combination provide reliable estimates of ocular dominance, which are strongly correlated across techniques both before and after deprivation. Moreover, while 15 min of monocular deprivation induce a larger shift of ocular dominance when measured using binocular combination compared to binocular rivalry, for both techniques, the shift in ocular dominance exhibits a strong dependence on the duration of monocular deprivation, with longer deprivation inducing a larger and longer-lasting shift in ocular dominance. Taken together, our results indicate that both binocular rivalry and binocular combination offer very consistent and reliable measurements of both ocular dominance and the effect short-term monocular deprivation.

1. Introduction

Short-term monocular deprivation (on the order of a few hours) temporarily shifts ocular dominance in favor of the deprived eye in adult humans (Baroncelli & Lunghi, 2021; Castaldi, Lunghi, & Morrone, 2020). This counter-intuitive boost of the deprived eye is thought to reflect a form of visual homeostatic plasticity (Mrsic-Flogel et al., 2007; Turrigiano & Nelson, 2004). The effect of short-term monocular deprivation is observed both at the perceptual (Lunghi, Burr, and Morrone 2011, 2013; Zhou et al., 2013) and at the neural level in the primary visual cortex, where opposite changes in visual evoked responses are observed for the deprived and non-deprived eye after short-term monocular deprivation (Binda et al., 2018; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015). In normal-sighted participants, the ocular dominance shift induced by 2–2.5 h of monocular deprivation peaks after eye-patch removal and then decays back to pre-deprivation levels within a couple of hours from the re-exposure to binocular vision (Lunghi et al., 2011, 2013; Zhou et al., 2013). Recent studies have shown that this transient effect of monocular deprivation can be stabilized for up to 6–7 h after deprivation by non-REM sleep (Menicucci, Lunghi, Zaccaro, Morrone, & Gemignani, 2022) and can become permanent in adult amblyopic patients (Lunghi, Sframeli, et al., 2019), indicating that this form of visual homeostatic plasticity can be useful for the development of new therapeutic strategies for sight restauration in adult humans. During the past decade, several studies have investigated the multifaceted characteristics of short-term ocular dominance plasticity. For example, several studies have shown that the effect of short-term monocular deprivation is modulated by non-visual processes such as energy metabolism (Animali et al., 2023; Daniele et al., 2021; Lunghi, Daniele, et al., 2019), physical exercise (Lunghi & Sale, 2015; Virathone, Nguyen, Dobson, Carter, & McKendrick, 2021; Zhou, Reynaud, & Hess, 2017), cholinergic potentiation (Sheynin et al., 2019), and sleep (Menicucci et al., 2022). Other studies have investigated the impact of different deprivation techniques, such as CFS (Kim et al., 2017), selective deprivation of Fourier phase from the input of one eye (Bai et al., 2017), varying the spatial image content of one eye (Zhou,

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Reynaud, & Hess, 2014), and kaleidoscopic deprivation (Ramamurthy & Blaser, 2018). Finally, various brain imaging techniques have been used to characterize the effect of short-term monocular deprivation on the visual system, including fMRI (Binda et al., 2018), MRS (Lunghi, Emir, et al. 2015), EEG (Lunghi, Berchicci, et al., 2015), and MEG (Chadnova et al., 2017).

To quantify ocular dominance and measure its change after short-term monocular deprivation most studies used one of two behavioral approaches: binocular rivalry (Levelt, 1965) and binocular combination (Blake & Fox, 1973). These two techniques rely on different mechanisms of binocular vision: interocular competition for binocular rivalry (Alais & Blake, 2005; Blake & Logothetis, 2002; Levelt, 1965) and interocular cooperation for binocular combination (Blake & Fox, 1973; Blake, Sloane, & Fox, 1981; Cogan, 1987; Ding & Sperling, 2006; Huang, Zhou, Zhou, & Zhong-Lin, 2010; Kwon et al., 2014). In binocular rivalry (Alais & Blake, 2005; Platonov & Goossens, 2014; Xu, He, & Ooi, 2011; Blake, 1989; Levelt, 1965) two incompatible stimuli are displayed separately to each eye, and the participant's perception alternates between the two stimuli. The binocular rivalry dynamic therefore relies on interocular inhibition and mutual suppression between the eyes (Alais, 2012; Blake, 1989, 2022; Blake & Logothetis, 2002; Tong et al., 2006). In binocular combination (Blake & Fox, 1973; Blake et al., 1981; Cogan, 1987; Ding & Sperling, 2006; Huang et al., 2010) two compatible but slightly different stimuli are presented independently to each eye. The two stimuli are fused into a coherent binocular percept, which is dominated by the visual feature presented to the dominant eye. Binocular combination relies on mutual integration and comparison of the images from each eye to form a weighted average of the monocular stimuli, which has been modeled through a multi-pathway contrast gain control model (Ding & Levi, 2017; Ding & Sperling, 2005; Huang, Zhou, Lu, & Zhou, 2011) involving both inhibition and excitation between the eyes.

Despite the fact that these two techniques rely on different aspects of binocular vision, their measurements of ocular dominance in normal sighted individuals correlate (Han et al., 2018; Yan et al., 2021), and they have so far been used interchangeably to measure the effect of short-term monocular deprivation (Bai, Dong, He, & Bao, 2017; Binda et al., 2018; Kim, Kim, & Blake, 2017; Lunghi, Burr, & Morrone, 2011, 2013; Lunghi, Emir, Morrone, & Bridge, 2015; Min et al., 2022; Min, Baldwin, & Hess, 2019; Sheynin et al., 2019; Spiegel, Baldwin, & Hess, 2017; Wang, McGraw, & Ledgeway, 2020; Yao et al., 2017; Zhou, Baker, Simard, Saint-Amour, & Hess, 2015; Zhou, Clavagnier, & Hess, 2013; Binda & Lunghi, 2017). While it has been established that both techniques can capture the effect of short-term monocular deprivation (namely, the ocular dominance shift in favor of the deprived eye), it is important to compare how they capture the variations of this effect induced by external factors.

Some discrepant results have been reported by independent studies using either technique: for example, the effect of short-term monocular deprivation is modulated differently for chromatic and achromatic gratings when measured using binocular rivalry (Lunghi, Burr, & Morrone, 2013) but not when measured using binocular combination (Zhou, Reynaud, Kim et al., 2017), and a similar difference has been found regarding the effect of physical exercise in modulating the effect of monocular deprivation (Lunghi & Sale, 2015; Zhou, Reynaud, & Hess, 2017). One study (Bai et al., 2017) conclusively showed that the deprivation of Fourier phase information from one eye induces an ocular dominance change when measured by binocular rivalry, but not when measured by binocular combination. These discrepancies raise the question of whether the two techniques capture different aspects of the effect of monocular deprivation, relying on separate neural mechanisms.

To address this important issue, here we directly compare the effect of short-term monocular deprivation on ocular dominance measured by either binocular rivalry or binocular combination in the same group of participants. To further compare the two techniques, we also measure the modulation of the effect by the duration of deprivation (15 or 120 min) for each technique.

2. Material and methods

2.1. Participants

25 adult volunteers (19 females, average age (mean ± sd) 26.9 ± 5.4), including the authors C.L., M.P. and A.P., participated in the study. All had normal or corrected-to-normal vision (measured with ETDRS charts) and, except the authors, all were naive to the purpose of the study.

2.2. Ethics statement

The experimental protocol was approved by the local ethics committee (Comité d'éthique de la Recherche de l'université Paris Descartes, CER-PD:2019-16-LUNGHI) and was performed in accordance with the Declaration of Helsinki (DoH-Oct2008). All participants gave written informed consent. Participants were reimbursed for their time at a rate of 10€ per hour.

2.3. Apparatus and stimuli

The experiment took place in a dark and quiet room. Experiments were run using a PC (Alienware Aurora R8, Alienware Corporation, Miami, Florida, USA) and a NVIDIA graphics card (GeForce RTX2080, Nvidia Corporation, Santa Clara, California, USA).

The stimuli were viewed through a custom-built mirror stereoscope. Participants' head was stabilized using a forehead and chin rest positioned at a distance of 57 cm from the screen. The display was a 24-inch LCD monitor (BenQ XL2420Z: BenQ, Taipei, Taiwan) with a 144 Hz maximum refresh rate and a resolution of 1920 × 1080 pixels such that each pixel subtended 0.028°, or 1.69 min of arc. The software tools (Psychtoolbox and Psychopy) and the monitor resolution allowed us to specify the monochrome stimuli to a resolution of 256 levels of gray (8-bit encoding of luminance values). We used a Minolta CS100A photometer (Konica Minolta Inc., Tokyo, Japan) to measure and calibrate (via gamma correction) the luminance profile of our screen and to ensure all our stimuli were reliably presented.

Monocular deprivation was performed through eye-patching of the dominant eye (defined as the eye showing longer dominance duration in binocular rivalry). The eye-patch was custom built and made of a translucent plastic material that allowed light to reach the retina (attenuation 15%) but no pattern information. Observers spent the monocular deprivation time in the lab, where they were free to perform their normal activities, such as working, reading, and walking outside. Monocular deprivation was performed either in the morning or the afternoon, after participants had eaten breakfast or lunch.

2.3.1. Binocular rivalry

The visual stimuli were generated in MATLAB (R2020b, The MathWorks Inc., Natick, MA) using PsychToolbox (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007) and consisted of 2 sinusoidal gratings (orientation: ±45°, spatial frequency: 2 cpd, contrast: 50%) presented on a uniform grey background (luminance: 110 cd/m2, CIE x = 0.305, y = 0.332) in a circular window (diameter: 2°) in central vision. A central red fixation point and a common white encompassing square frame were superimposed to the gratings stimulus to facilitate dichoptic fusion (Fig. 1A).

Before each 90 sec experimental block, a binocular fixation frame was presented: a central fixation dot and larger square frame (5° × 5°), with two small monocular rectangles (0.25° × 0.5°) – top and left edge of the frame for the left eye and bottom and right edge of the frame in the right eye - pointing from the edge of the frame towards the fixation dot (see the frames surrounding the visual stimuli in Fig. 1A). The frames were presented until the participant had achieved stable vergence, characterized by the binocular perception of one frame with aligned rectangles facing the fixation dot.

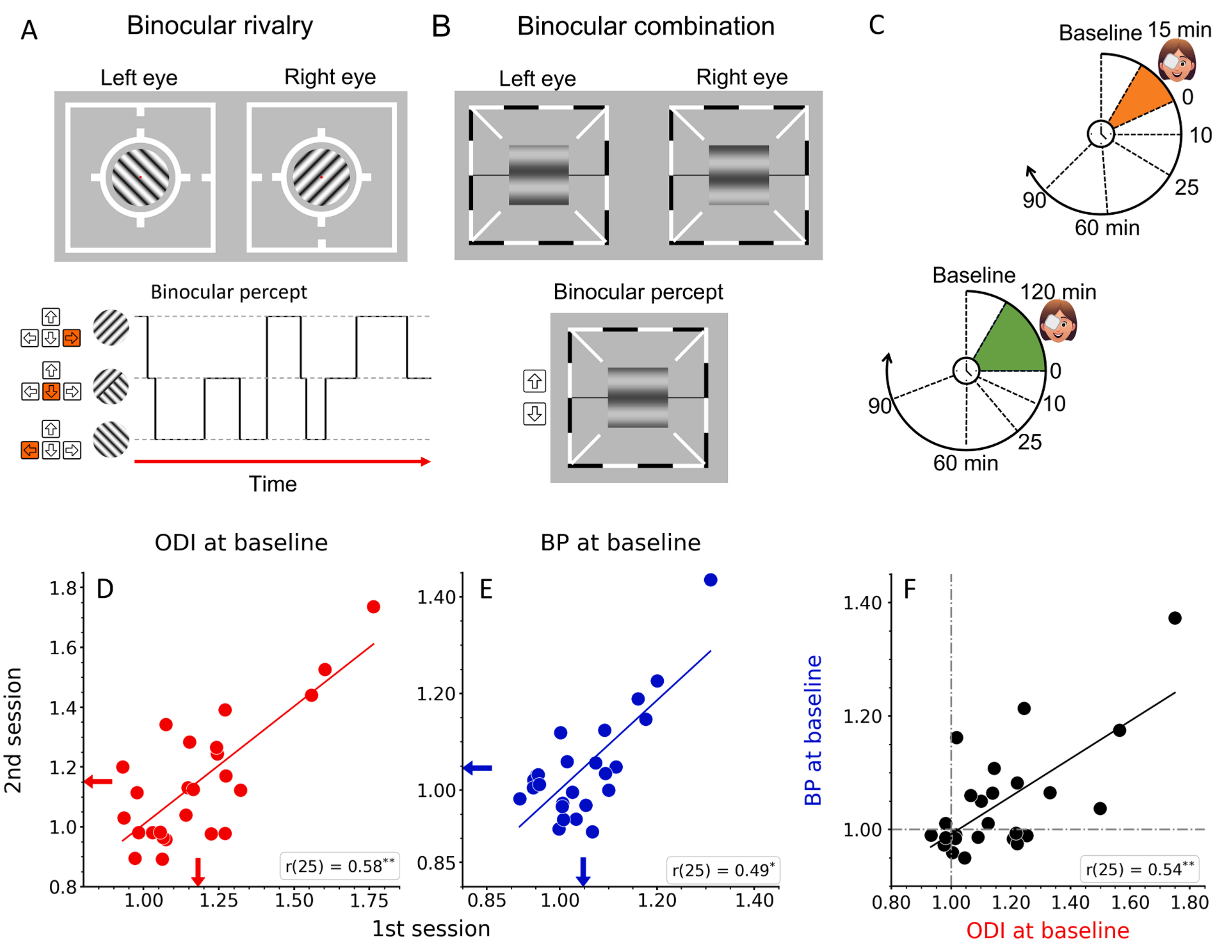

Fig. 1. Experimental design and ocular dominance assessment at baseline. A: Binocular rivalry (BR). Visual stimuli were orthogonal gratings presented dichoptically (top panel). Observers reported their visual perception using the computer keyboard (bottom panel). B: Binocular combination (BC). Visual stimuli were sinusoidal gratings having a 45° phase difference presented dichoptically (top panel). Participants reported the phase of the cyclopean grating adjusting the elevation of a probe line (bottom panel). C: Monocular deprivation conditions (MD): MD was achieved by patching the participants' dominant eye for either 15 or 120 min. 5 OD measurements were performed after eye-patch removal: 0 min, 10 min, 25 min, 60 min, and 90 min after the end of deprivation. D: Correlation between OD measurements measured by binocular rivalry obtained in two independent sessions. Arrows on the axes indicate the mean ODI for each session. E: Same as D, but for the binocular combination task. F: Correlation between baseline OD measured by binocular rivalry and binocular combination. *** = $p < 0.001$, Spearman's rank correlation coefficient.

2.3.2. Binocular combination

The visual stimuli were generated in Python (v3.8, python.org) using PsychoPy version 2021.2.3 (Peirce, 2007; Peirce, 2008) and consisted of 2 horizontal sine-wave gratings subtending 3.5° × 3.5° (Fig. 1B). The luminance profiles of the gratings in the left and right eyes can be described by the following equations:

$$Lum_L(x) = L_0\left[1 - \delta C_0 \cos\left(2\pi f x \mp \frac{\theta}{2}\right)\right] \quad (1)$$

$$Lum_R(x) = L_0\left[1 - C_0 \cos\left(2\pi f x \pm \frac{\theta}{2}\right)\right] \quad (2)$$

or

$$Lum_L(x) = L_0\left[1 - C_0 \cos\left(2\pi f x \mp \frac{\theta}{2}\right)\right] \quad (3)$$

$$Lum_R(x) = L_0\left[1 - \delta C_0 \cos\left(2\pi f x \pm \frac{\theta}{2}\right)\right] \quad (4)$$

Where $L_0 = 110$ cd/m^2 is the background luminance, $C_0 = 50\%$ is the base contrast of the gratings, $\delta \in [0.2, 0.5, 0.7, 1.0, 1.2]$ is the interocular contrast ratio, $\theta = 45°$ is the total phase difference between the gratings, and $f = 0.5$c/d is the spatial frequency of the gratings (Fig. 1B).

To facilitate dichoptic fusion, the grating in each eye was surrounded by a larger (6° × 6°), high-contrast frame with clearly marked white diagonals (vergence lines, see Fig. 1B).

Before each stimulus presentation, a binocular fixation cross (1.25° × 1.25°) and monocular fixation dots (0.22° diameter) - in the 1st and 3rd quadrants in the left eye and 2nd and 4th quadrants of the right eye - were presented until participants had achieved stable vergence, characterized by one high contrast frame and one cross with 4 balanced dots in its corners.

The monocular gratings were presented in two phase conditions ($\frac{\theta}{2}$ in the left eye and $-\frac{\theta}{2}$ in the right eye; $-\frac{\theta}{2}$ in the left eye and $\frac{\theta}{2}$ in the right eye), two base contrast conditions (contrast(left eye) = C_0 and contrast (right eye) = δC_0; contrast(left eye) = δC_0 and contrast(right eye) = C_0) and 5 interocular contrast ratios ([0.2, 0.5, 0.7, 1.0, 1.2]), for a total of $2 \times 2 \times 5 = 20$ distinct stimuli configurations. The interocular contrast ratio is the ratio of the contrasts of the stimuli presented in each eye: when $\delta = 0.2$, one eye is presented with $C_0 = 50\%$ (base) contrast and the other with $C = 10\%$ contrast, such that: $\delta = \frac{C}{C_0} = \frac{0.1}{0.5} = 0.2$. The maximum contrast displayed in either eye was $C_{max} = 1.2{*}C_0 = 1.2{*}50\% = 60\%$ contrast. An example showing the 4 possible phase/contrast conditions is shown in Supplementary Fig. 1.

Baseline measurements consisted of 200 trials (10 repetitions per stimuli configuration). After deprivation each block consisted of 100 trials (5 repetitions per stimuli configuration). This allowed us to match the duration of the post-deprivation blocks (~8 min) in both the binocular rivalry and binocular combination tasks.

2.4. Procedures

Each participant took part in 4 independent experimental conditions (in a counterbalanced order) in which ocular dominance (OD) was tested either by means of binocular rivalry (BR) or binocular combination (BC) before and after either 15 or 120 min of monocular deprivation (Fig. 1C). Therefore, the four experimental conditions were: BR15, BR120, BC15, and BC120 (the order of the condition was counterbalanced across participants).

After eye-patch removal, ocular dominance was reassessed five times at regular intervals: 0 min, 10 min, 25 min, 60 min, and 90 min after the removal of the eye-patch.

Each ocular dominance measurement lasted about 8 min, leaving at least a two-minute rest period between the measurements.

2.4.1. Binocular rivalry

In the binocular rivalry (BR) task, participants were asked to report in real time the dominant visual percept (left-tilted, right-tilted, or mixed) by continuously pressing the left or right arrow on a keyboard for complete dominance of the right-tilted and left-tilted gratings and the down arrow key for mixed percepts.

One measurement consisted of 4 90-seconds block, with a 120-seconds break between the 2nd and 3rd blocks, and 10 s breaks between the 1st and 2nd and 3rd and 4th blocks. The orientation associated to each eye was swapped at each block to avoid adaptation.

2.4.2. Binocular combination

In the binocular combination (BC) task, participants were asked to report the perceived phase of the cyclopean grating by adjusting a grey one-pixel thick probe to the darkest part of the grating (Fig. 1B).

The gratings were kept on screen until the participants validated their response through a keypress, at which point the vergence frame with the dichoptic cross was presented again until the participants indicated that they had reached proper vergence by another keypress, starting the next trial.

Data were collected for the 20 different stimuli configurations in a randomized order, with a 60-seconds break after 100 trials during the baseline measurement.

2.5. Analyses

2.5.1. Binocular rivalry

For each experimental session, we computed an Ocular Dominance Index (ODI) quantifying ocular dominance:

$$ODI = \frac{T_{deprived}}{T_{nondeprived}} \tag{5}$$

Where T represents the total time spent by the observers reporting the complete dominance of the visual stimulus presented either to the deprived or non-deprived eye.

The effect of monocular deprivation (MD effect) on ocular dominance was measured by the difference between the logarithms of the baseline and post-deprivation ODI, as described by:

$$MD\ \ effect = \log_{10}(ODI_{post}) - \log_{10}(ODI_{Baseline}) \tag{6}$$

2.5.2. Binocular combination

The responses we collected in the binocular combination task are the perceived phase of the binocular percept, denoted Φ. The perceived phase depends on the three parameters described in section 2.3.2: the interocular contrast ratio (denoted δ, which can take five values: [0.2, 0.5, 0.7, 1.0, 1.2]), the eye to which the base contrast C_0 was presented (denoted C_{0D} when C_0 was presented to the deprived eye and C_{0ND} when C_0 was presented to the non-deprived eye), and the phase configuration ($\pm\theta$) applied to the stimuli. The responses for our 20 stimulus conditions were therefore defined as:

$$\Phi(\delta;\ C_{0D}\ ;\ \pm\theta) = \Phi_{deprived}(\delta\ ;\ \pm\theta),$$

$$\Phi(\delta;\ C_{0ND}\ ;\pm\theta) = \Phi_{nondeprived}(\delta;\pm\theta);$$

Where $\Phi_{deprived}$ and $\Phi_{nondeprived}$ are the perceived phases of the grating when the base contrast is presented to the deprived or non-deprived eye respectively.

We presented each stimulus configuration *Nrep* times (Nrep = 10 in the baseline measurements, then Nrep = 5 after monocular deprivation), which we averaged to increase the reliability of our measurement, giving us 20 unique values of perceived phase such that:

$$\Phi_{deprived}(\delta;\ \pm\theta) = \frac{\sum_{i=1}^{Nrep}\Phi_{deprived,\ i}(\delta;\ \ \pm\theta)}{Nrep} \tag{7}$$

$$\Phi_{nondeprived}(\delta;\ \ \pm\theta) = \frac{\sum_{i=1}^{Nrep}\Phi_{nondeprived,\ i}(\delta;\ \ \pm\theta)}{Nrep}$$

For both $\Phi_{deprived}$ and $\Phi_{nondeprived}$, for every given interocular contrast ratio δ the two different phase configurations ($\pm\theta$) were introduced to prevent vertical position bias. As such, we averaged the responses from each configuration to remove the phase configuration dependence of our perceived phase data:

$$\Phi_{deprived}(\delta) = \frac{\Phi_{deprived}(\delta;+\theta) - \Phi_{deprived}(\delta;-\theta)}{2} \tag{8}$$

$$\Phi_{nondeprived}(\delta) = \frac{\Phi_{nondeprived}(\delta;+\theta) - \Phi_{nondeprived}(\delta;-\theta)}{2}$$

At this point, we have 10 unique perceived phase values for each participant: two values for each of the 5 interocular contrast ratios, one obtained when the deprived eye was presented with C_0 (Φ_{deprived}), and one when the non-deprived eye was presented with C_0 ($\Phi_{\mathrm{nondeprived}}$). These values were plotted to make a perceived phase vs interocular contrast ratio (PvR) curve for each eye, from which we derived the balance point of binocular phase combination by fitting a multipathway contrast gain control model (Huang et al., 2009, 2011; Yan et al., 2021):

$$\widehat{\Phi}_{deprived} = 2\tan^{-1}\left[\frac{\eta^{1+\gamma}-\delta^{1+\gamma}}{\eta^{1+\gamma}+\delta^{1+\gamma}}\tan\left(\frac{\theta-\beta}{2}\right)\right] \tag{9}$$

(Base contrast in deprived eye)

$$\widehat{\Phi}_{nondeprived} = 2\tan^{-1}\left[\frac{1-(\eta\delta)^{1+\gamma}}{1+(\eta\delta)^{1+\gamma}}\tan\left(\frac{\theta-\beta}{2}\right)\right] \tag{10}$$

(Base contrast in non-deprived eye)

Where $\widehat{\Phi}_{deprived}$ and $\widehat{\Phi}_{nondeprived}$ are the predicted phases of the cyclopean grating when the base contrast is presented to the deprived or non-deprived eye respectively, η is the balance point (BP) at which the two eyes contribute equally in binocular combination, δ is the interocular contrast ratio, γ is the system nonlinearity, θ is the phase difference between the monocular gratings (fixed at 45°), and β is the perceived phase bias (a free parameter which helps to accommodate participants fixed response biases in perceived phase reporting). An η of 1.0 means perfect balance between the eyes; $\eta < 1.0$: non-deprived eye dominates perception; $\eta > 1.0$: deprived eye dominates perception.

The model fitting was implemented through the curve_fit function of the Scipy package in Python, which minimizes $\sum(\Phi_{predicted} - \Phi_{measured})^2$ through a non-linear least-square procedure, and evaluates the goodness of fit through the r^2:

$$r^2 = 1.0 - \frac{\sum\left(\Phi_{predicted} - \Phi_{measured}\right)^2}{\sum\left[\Phi_{measured} - mean(\Phi_{measured})\right]^2} \tag{11}$$

To increase the robustness of this balance point estimate, we resampled the initial data (with replacement) 2000 times and performed the curve fitting on the resampled data. The reported values for the model parameters for each participant are the median values from this bootstrap procedure.

For the baseline measurements, γ was bounded such that $\gamma > 0$ to keep the parameters within reasonable ranges with respect to previous results from the literature.

The average and individual PvR curves obtained before and after 120 min of monocular deprivation are reported in Supplementary Figs. 2 and 3.

The effect of monocular deprivation (MD effect) on ocular dominance was measured by the difference between the logarithms of the baseline and post-deprivation balance point (BP) values, as described by this equation:

$$MD\,effect = \log_{10}\left(BP_{post}\right) - \log_{10}\left(BP_{Baseline}\right) \tag{12}$$

2.5.3. *Linear fit of the monocular deprivation effect*

For each of our 25 participants we measured the MD effect at 5 different time points, producing a distribution of 25 values at each time point. These 25 values were then averaged, and this average was used to fit a linear model of the effect of monocular deprivation over time:

$$f(t) = a^{*}t + b \tag{13}$$

This fitted curve was then used to compute the area under the curve, which provides an indication of the total effect of monocular deprivation on ocular dominance.

2.5.4. *Area under the curve*

To compute the area under the curve, 10 000 repetitions of bootstrapping were performed on the MD effect data, re-fitting the randomly resampled data (with replacement) with a linear fit as described above. Then we computed the area under the curve of each linear fit using the "auc" function from the scikit-learn package in Python.

2.6. *Statistics*

2.6.1. *Correlations*

The correlations we present are computed using the Scipy.stats Python package's "spearmanr" function, which computes Spearman's rank correlation coefficient and the p-value for testing non-correlation. We chose Spearman's correlation coefficient for its robustness to outliers. To compare different sessions measured using the same technique we used Bland-Altman plots, which describe the mean difference between sessions from individual participants against the average over these two sessions.

2.6.2. *ANOVA*

To compare the effect of the two monocular deprivation durations, we performed a repeated-measure ANOVA analysis using JASP (JASP Team (2022), JASP (Version 0.16.3)). For each technique (binocular rivalry and binocular combination), we performed a 2X5 repeated-measures ANOVA with the factors MD_duration (15 and 120 min) and TIME (5 experimental blocks acquired after eye patch removal). The Greenhouse-Geisser correction was applied when appropriate (the assumption of sphericity was violated for the within subject effect of F2 and the interaction of F1 × F2, see Supplementary tables 1 and 2 for details).

2.6.3. *Post-hoc tests*

All post-hoc tests were conducted using the Scipy package in Python. We used one-sample t-tests ("scipy.stats.ttest_1samp") to compare the effects of monocular deprivation against 0, and applied Bonferroni's correction for multiple comparisons through the "multipletests" function of the Statsmodels package in Python ("statsmodels.stats.mutlitest.multipletests").

2.6.4. *Bootstrap*

To compare statistically the area under the curve (AUC) of the monocular deprivation effect between the two deprivation durations, we performed a bootstrap analysis.

We recomputed 10 000 times the linear fit of the monocular deprivation effect curves from a resampled distribution of the 25 points from which we compute the average monocular deprivation effect at each time point.

The distributions of the bootstrapped AUC values (presented in the histograms in Fig. 2C and D) were then statistically compared by performing a two-tail bootstrap sign-test.

3. Results

We tested the effect of either 15 or 120 min of monocular deprivation (MD) on ocular dominance (Fig. 1C) measured either by means of binocular rivalry (BR, Fig. 1A) or binocular combination (BC, Fig. 1B) in healthy adult humans.

3.1. *Binocular rivalry and binocular combination provide reliable estimates of ocular dominance at baseline*

We first assessed the test–retest reliability of each technique (BR and BC) in estimating ocular dominance by comparing the ocular dominance measurements obtained before monocular deprivation for the two independent experimental sessions (either the 15 min or the 120 min MD condition). For binocular rivalry, ocular dominance was estimated by computing an ocular dominance index (ODI, see Equation (5) based on the dominance duration of each eye as reported by the observers. For binocular combination, ocular dominance was estimated as the interocular contrast ratio necessary to perceive a cyclopean grating with a phase = 0° (balance point, BP, see *Analysis* in the Methods section for details). We found that both binocular rivalry (Fig. 1D) and binocular combination (Fig. 1E) provided a reliable estimation of ocular dominance, as measurements obtained in the two separate experimental sessions were highly correlated across participants (BR: mean ± s.e.m. ODI-session 1 = 1.151 ± 0.043, mean ± s.e.m. ODI-session 2 = 1.181 ± 0.042, Spearman's correlation r = 0.576, p = 0.003; BC: mean ± s.e.m. BP-session 1 = 1.045 ± 0.023, mean ± s.e.m. BP-session 2 = 1.048 ± 0.018, Spearman's correlation r = 0.488, p = 0.013), indicating a strong test–retest reliability for both techniques. To further estimate the test–retest reliability of each technique, we also computed Bland-Altman plots (Supplementary figure 4), which show that mean of the differences between the two sessions is not significantly different from 0 (95% CI of the mean(s1-s2) for each technique: BR = [-0.024; 0.084]; BC = [-0.026; 0.032]; *t*-test of mean(distribution of differences) vs 0: BR: t(24) = 1.06, p = 0.30; BC: t(24) = 0.19, p = 0.85).

We further compared the ocular dominance estimates across the two experimental techniques (BR and BC) by averaging for each technique the baseline measurements obtained for each participant. We found a strong correlation (Spearman's r = 0.538, p = 0.005) between ocular dominance estimates obtained with BR and BC (Fig. 1F) indicating that both techniques measure related aspects of ocular dominance at baseline.

3.2. *The change in ocular dominance induced by monocular deprivation depends strongly on the duration of deprivation*

To investigate the effect of the duration of deprivation on short-term visual homeostatic plasticity, we measured ocular dominance before and after either 120 or 15 min of monocular deprivation. To quantify the

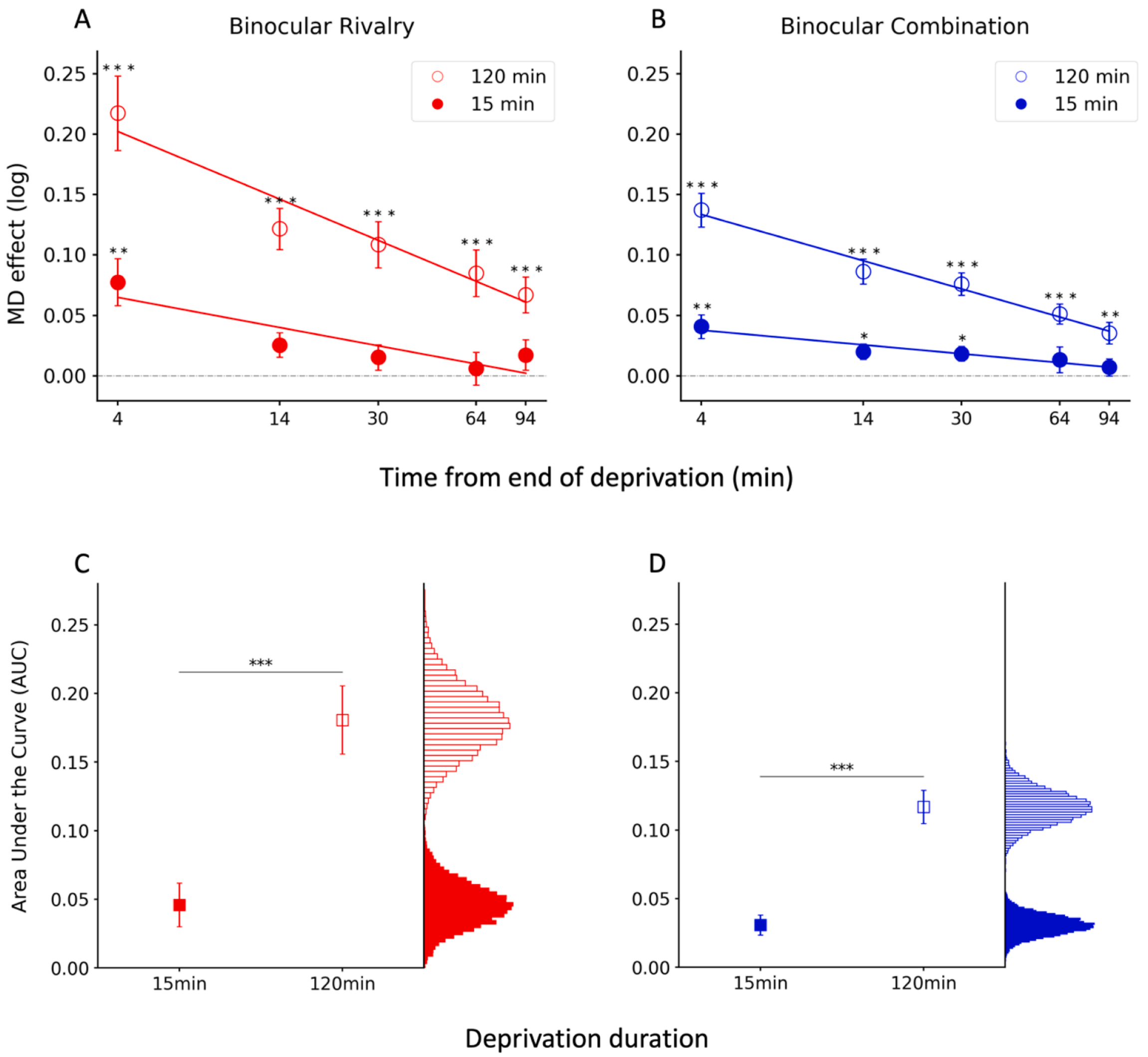

Fig. 2. Effect of monocular deprivation on ocular dominance. A: Effect of 120-min (empty symbols) and 15-min (solid symbols) of monocular deprivation on ocular dominance as measured by Binocular Rivalry. Error bars represent 1 ± SEM. (*** = $p < 0.001$, ** = $p < 0.01$, *=$p < 0.05$, *t*-test against 0, Bonferroni correction for multiple comparisons). B: Same as A, but for the binocular combination condition. C: Area under the curve of the MD effect measured after 120-min (empty symbol) and 15-min (solid symbol) of MD for the binocular rivalry condition. The histograms show the distribution of the 10,000 bootstrap values for the 120 (empty bars) and 15 min (solid bars) of MD. Error bars represent 1 ± SEM (bootstrap). (*** = $p < 0.001$, two-tailed bootstrap sign-test). D: Same as C, but for the binocular combination condition.

monocular deprivation effect, we computed the difference between the logarithm of the ocular dominance estimate (ODI for binocular rivalry, BP for binocular combination) obtained at baseline and after monocular deprivation (See Equations (6) and (12)). We found that, for both techniques and both deprivation durations, monocular deprivation induced an ocular dominance shift in favor of the deprived eye, consistent with previous findings (Lunghi, Burr, & Morrone, 2011). The decay of the effect (on a log–log scale) was well modeled by a linear fit (see Equation (13), all $R^2 > 0.8$).

For both binocular rivalry (Fig. 2A) and binocular combination (Fig. 2B), the effect of monocular deprivation was highly affected by the duration of deprivation. Specifically, 120 min of monocular deprivation induced a larger and more long-lasting shift of ocular dominance compared to 15 min of monocular deprivation. This was confirmed by a 2 (MD-duration) × 5 (TIME) repeated-measures ANOVA: for both BR and BC we found a significant main effect of the factor MD-duration (BR: $F(1, 24) = 35.838$, $\eta^2 = 0.278$, $p < 0.001$; BC: $F(1, 24) = 49.087$, $\eta^2 = 0.295$, $p < 0.001$), a significant main effect of the factor TIME (BR: $F(1, 4) = 25.625$, $\eta^2 = 0.195$, $p < 0.001$; BC: $F(1, 4) = 24.624$, $\eta^2 = 0.191$, $p < 0.001$) and a significant interaction between the two factors (BR: $F(1, 4) = 5.218$, $\eta^2 = 0.028$, $p = 0.004$; BC: $F(1, 4) = 9.149$, $\eta^2 = 0.051$, $p < 0.001$). Post-hoc tests revealed that for the 120 min monocular deprivation condition, the MD effect was significantly>0 for all the post-MD measurements (up to 90 min following eye-patch removal) for both BR and BC (all $ps < 0.003$, see Supplementary table 4). In the 15 min monocular deprivation condition, the MD effect was significantly larger than 0 only for the first post-MD measurement (0–8 min after eye-patch removal) for binocular rivalry, and for the first three measurements after MD (up to 34 min following eye-patch removal) for binocular combination (see Supplementary table 3 for statistical details). To further characterize the overall effect of monocular deprivation over time, we computed the area under the curve (AUC) of the linear fit for each experimental condition (Fig. 2C-D). This analysis confirmed that for both BR (Fig. 2C) and BC (Fig. 2D), 120 min of monocular deprivation induced a larger ocular dominance shift compared to 15 min of monocular deprivation (two-tailed bootstrap sign-test, $ps < 10^{-10}$). For both techniques, the effect induced by 120 min of deprivation was about 4 times larger than that induced by 15 min of deprivation (BR: mean ± sem AUC 120 min = 0.1801 ± 0.0245, mean ± sem AUC 15 min = 0.0459 ± 0.0159; BC: mean ± sem AUC 120 min = 0.1168 ± 0.0118, mean ± sem AUC 15 min = 0.0310 ± 0.0073).

Finally, we found that, in binocular rivalry, the proportion of mixed percept did not vary after monocular deprivation (Supplementary figure 5), and that, across participants, the proportion of mixed percepts measured at baseline did not correlate with the effect of 120 min of monocular deprivation measured by either BR or BC, nor for 15 min as measured by BR, although we found a negative correlation between the proportion of mixed percepts measured at baseline the effect of 15 min of monocular deprivation as measured by BC (Supplementary figure 6).

3.3. Correlations between the monocular deprivation effect measured independently by binocular rivalry and binocular combination

Having shown that binocular rivalry and binocular combination provide correlated measures of ocular dominance at baseline and that both show the same modulation of the monocular deprivation effect, we investigated the correlation between the two techniques in assessing the effect of short-term monocular deprivation. To this end, we compared both the monocular deprivation effect (Equations (6) and (12)) and the raw ocular dominance measurements (ODI for binocular rivalry and BP for binocular combination) assessed by each technique after either 120 or 15 min of monocular deprivation (see Fig. 3). For each technique, we computed the average monocular deprivation effect ($\log_{10}$ of the arithmetic average of all experimental blocks tested after the removal of the eye patch). We found that for both 15 and 120 min of monocular deprivation, the mean ocular dominance measurements across the post-deprivation sessions correlate strongly across participants (15 min MD: Spearman's r = 0.512, p = 0.0089; 120 min MD: Spearman's r = 0.672, $p < 0.001$, Fig. 3A-B). This reinforces our finding that BR and BC provide comparable assessments of ocular dominance (Fig. 1F), even when ocular dominance is altered by an experimental manipulation such as short-term monocular deprivation.

Surprisingly, we also found that the monocular deprivation effect assessed by the two techniques does not correlate across participants for either deprivation duration (15 min MD: Spearman's r = 0.312, p = 0.129; 120 min MD: Spearman's r = 0.277, p = 0.180, Fig. 3C-D).

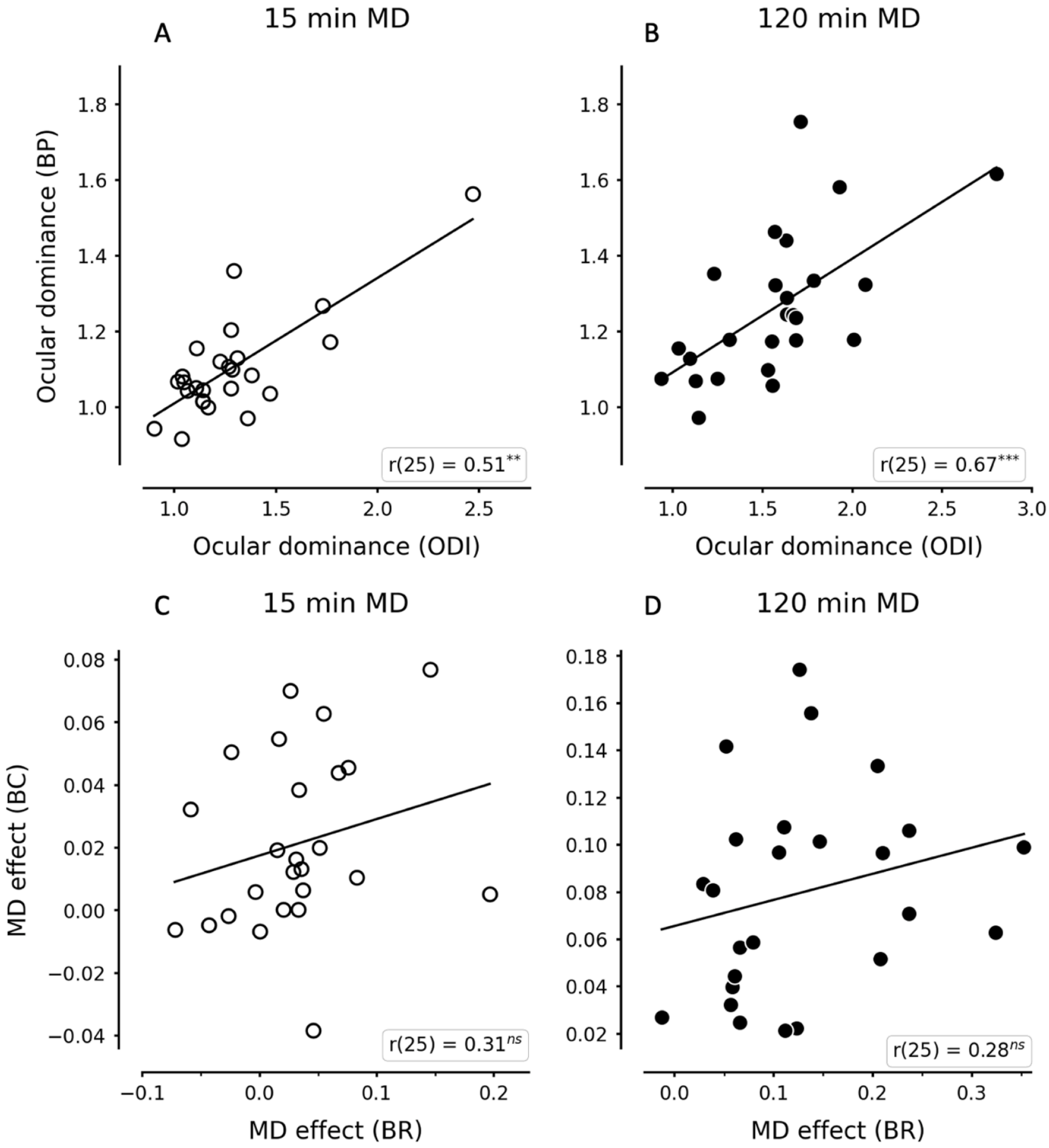

Fig. 3. Correlation between the effect of short-term monocular deprivation measured by binocular rivalry (BR) and binocular combination (BC). A: Scatter plot of the mean ocular dominance measured after 15 min of monocular deprivation (MD) by means of BR (ODI) vs. BC (BP). B: Same as A but for 120 min MD.C: Scatter plot of the mean MD effect measured after 15 min of MD by means of BR vs. BC. D: Same as C but for 120 min MD. ns = $p > 0.05$, *** = $p < 0.001$, Spearman's rank correlation coefficient.

4. Discussion

We directly compared the measurements of ocular dominance and its modulation by short-term monocular deprivation in the same participants assessed both by binocular rivalry (BR) and binocular combination (BC) techniques. Our results show that both techniques provide reliable estimates of ocular dominance, with a high test–retest reliability. Moreover, both techniques capture equally well the effect of short-term monocular deprivation and its modulation by the deprivation duration, with BC showing a higher sensitivity for very short monocular deprivation durations.

Binocular rivalry and binocular combination are mediated by different neural mechanisms. Binocular rivalry dynamics rely on interocular inhibition and mutual suppression between the eyes (Blake, 1989; Tong et al., 2006), in which monocular signals reciprocally inhibit each other at early stages of visual processing (Alais, 2012; Blake, 1989), but also through interactions with feedback from later areas and higher-level pattern grouping (Tong et al., 2006). On the other hand, binocular combination relies on integration and comparison of the images from each eye to form a weighted average of the monocular stimuli, which has been modeled through a multi-pathway contrast gain control model (Ding & Levi, 2017; Ding & Sperling, 2005; Huang et al., 2011). Binocular combination therefore involves both inhibition and excitation between the eyes (Huang, Zhou, Zhou, & Zhong-Lin, 2010). In light of the differences between these two phenomena, it is possible that complex effects acting on heterogeneous neural mechanisms might be captured in a different way when measured by either BR or BC, giving rise to potentially different results. Short-term visual homeostatic plasticity induced by monocular deprivation may be one of these cases: while monocular deprivation affects evoked responses in a similar way at different stages of visual processing (Binda et al., 2018; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015), boosting the responses of the deprived eye and decreasing the non-deprived eye activity, it also involves other multifaceted and complex neural mechanisms, including GABAergic inhibition (Lunghi, Emir, et al. 2015), other neuromodulators (Binda & Lunghi, 2017), energy metabolism (Animali et al., 2023; Daniele et al., 2021; Lunghi, Daniele, et al., 2019) and non-REM sleep (Menicucci et al., 2022).

We show that the boost of the deprived eye induced by short-term monocular deprivation is modulated in identical ways by the duration of deprivation when measured with BR and BC: for both techniques, longer deprivations induce a stronger and longer lasting effect, in line with previous results (Lunghi, Burr, & Morrone, 2013; Min et al., 2022). This difference in both the amplitude and the recovery of the effect induced by different deprivation durations indicates that this effect builds up over the duration of deprivation. We also find that the difference in amplitude of the effect induced by 15 min and 120 min deprivation is the same for both techniques ($\sim$4 times larger for 120 min vs 15 min). This result indicates that the change in ocular dominance induced by monocular deprivation affects the ocular dominance mechanisms underlying each technique in a qualitatively similar fashion, suggesting that short-term monocular deprivation changes visual cortical activity at a large scale. This is consistent with neuroimaging studies showing that monocular deprivation induces a transient change in evoked responses at various stages of visual analysis, from the visual thalamus (Kurzawski et al., 2022), to V1 and higher level visual areas (Binda et al., 2018; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015).

Our results also show that very short (15 min) monocular deprivation seems to have a larger effect on ocular dominance measured using binocular combination compared to binocular rivalry (for combination a small shift in ocular dominance is measurable for up to 34 min after deprivation, while for rivalry, the ocular dominance shift disappears 10 min after deprivation). This result suggests that the excitatory circuits involved in binocular combination might be more sensitive to deprivation at the initial stages of the effect, showing a faster dynamic compared to the inhibitory circuits involved in binocular rivalry. This difference in the dynamic of the monocular deprivation effect might potentially be relevant to interpret the discrepancies between the effect measured by BR and BC found in previous studies (Bai, Dong, He, & Bao, 2017; Lunghi, Burr, & Morrone, 2013; Lunghi & Sale, 2015; Zhou, Reynaud, Kim, Mullen, & Hess, 2017; Zhou, Reynaud, & Hess, 2017).

Our results also confirmed previous observations (Han et al., 2018; Yan et al., 2021) that ocular dominance measurements obtained by binocular rivalry and binocular combination are strongly correlated in normal sighted participants. For example, Yan et al. (2021) reported a significant correlation between the ocular dominance measurements from binocular phase combination and binocular rivalry in the younger group of their cohort (age 22.2 ± 2.3 years, mean ± std). The age of our participants is close to the age of their young cohort (26.9 ± 5.4, mean ± std), we therefore replicate their findings, showing a similar correlation between the balance point of binocular combination and the dominance duration ratio of binocular rivalry ($r = 0.538$, $p = 0.005$). Importantly, we show that this correlation between balance point estimated from binocular combination and dominance duration ratio from binocular rivalry is entirely preserved after short-term monocular deprivation, thus, even though different aspects of binocular vision rely on potentially distinct neural mechanisms, biases in ocular dominance are captured equally well by BC and BR, suggesting that the mechanisms underlying ocular dominance are shared between the two techniques.

One surprising aspect of our result is the lack of correlation between the monocular deprivation effect measured by binocular rivalry and binocular combination despite the correlation between the ocular dominance estimates obtained both before and after deprivation. This lack of correlation between the effect measured by the two techniques might be due to the increase in noise when computing the MD effect (difference between baseline and post-deprivation ocular dominance measurements). Ocular dominance measurements at baseline and after monocular deprivation are correlated for both techniques (Supplementary Figure 7), indicating high co-variance between the variables used to compute the effect. In such case, the variance of the monocular deprivation effect may reflect measurement noise, rather than inter-individual variability (captured by the co-variance), possibly obscuring a correlation between the effects. An alternative interpretation of this result, is that the two techniques might capture different aspects of the monocular deprivation effect, perhaps more linked to inhibitory mechanisms in one case (binocular rivalry) and to excitatory mechanisms in the other case (binocular combination).

In summary, our results show that both binocular rivalry and binocular combination offer very consistent and reliable measurements of both ocular dominance and the effect short-term monocular deprivation, and the modulation of the effect by the deprivation duration. More studies comparing the processes of BR and BC with neuro-imaging techniques and monocular deprivation could provide important insight into how the homeostatic plasticity mechanisms involved in the effect of short-term monocular deprivation on ocular dominance impact the different mechanisms involved in binocular vision in humans.

CRediT authorship contribution statement

Antoine Prosper: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Martina Pasqualetti:** Investigation, Data curation, Formal analysis. **Maria Concetta Morrone:** Conceptualization, Methodology, Validation, Writing – review & editing. **Claudia Lunghi:** Conceptualization, Methodology, Validation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The full dataset generated during the current study and the analysis script used to process the data is available on the Zenodo repository: https://doi.org/10.5281/zenodo.8043798.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2023.108278.

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