Temporary monocular occlusion facilitates binocular fusion during rivalry

Yasha Sheynin
McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montréal, QC, Canada

Sébastien Proulx
McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montréal, QC, Canada

Robert F. Hess
McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montréal, QC, Canada

A few hours of monocular patching temporarily enhances the deprived eye’s contribution to binocular vision, constituting a form of adult brain plasticity. Although the mechanism for this plasticity is currently unknown, several imaging studies present evidence that monocular deprivation achieves its effects by changing excitatory–inhibitory balance in the visual cortex. Much of the past work on adult monocular patching utilized binocular rivalry to quantify the patching-induced shift in perceptual eye dominance, extracting periods of exclusive visibility (in which one eye’s signal is suppressed from perception) to assess each eye’s contribution to binocular vision while overlooking the occurrence of mixed visibility (in which information from both eyes is combined). In this paper, we discuss two experiments to investigate the effects of short-term monocular occlusion on the relative predominance of mixed and exclusive percepts during binocular rivalry. In addition to the known perceptual eye-dominance shift, we hypothesized patching would also increase the perception of mixtures during rivalry due to deprivation-induced changes in excitatory–inhibitory balance. Our data point to two previously unknown effects of monocular deprivation: (a) a significant increase in the overall fraction and median duration of mixed visibility during rivalry that is detectable up to at least an hour after removing the patch and (b) the overall fraction of superimposition; rather than piecemeal, mixed percepts are specifically enhanced after monocular deprivation. In addition to strengthening the contribution of the deprived eye, our results show that temporary monocular patching enhances the visibility of fused binocular percepts, likely the result of attenuated interocular inhibition.

Introduction

Short-term monocular deprivation (MD) is known to have several effects on adult human vision (see Baldwin & Hess, 2018, for an overview). MD, or patching, can shift perceptual eye dominance at the neural level (Hubel & Wiesel, 1970; Tso, Miller, & Begum, 2017). In childhood, long-term (>1 week) MD causes a shift in favor of the nondeprived eye, and temporarily patching an eye for a few hours in adulthood results in a shift in favor the deprived eye that is observable up to at least an hour after deprivation (Lunghi, Burr, & Morrone, 2011). The ability of the adult visual system to temporarily shift perceptual eye dominance points to a latent functional plasticity whose mechanism is currently unknown although there is empirical evidence implicating changes in excitatory–inhibitory (E-I) balance in V1 (Chadnova, Reynaud, Clavagnier, & Hess, 2017; Lunghi, Emir, Morrone, & Bridge, 2015).

Studies investigating the effects of MD on binocular vision generally measure perceptual eye dominance behaviorally with either binocular rivalry (Binda et al., 2017; Kim, Kim, & Blake, 2017; Lunghi et al., 2011; Lunghi, Emir, et al., 2015; Lunghi, Morrone, Secci, & Caputo, 2016) or binocular phase combination (Baldwin & Hess, 2018; Chadnova et al., 2017; Zhou, Baker, Simard, Saint-Amour, & Hess, 2015) tasks. For the purpose of the current paper, we focus on binocular rivalry. Binocular rivalry occurs when the eyes are presented separate incongruent images, and it is defined by perceptual alternations that shift perception from...
one eye’s image to the other over the course of presentation (see Blake & Logothetis, 2002, for a review). Studies that use binocular rivalry to measure perceptual eye dominance infer the contributions of the two eyes from the degree to which one eye suppresses the other when competing, or rivaling, for perception.

Although binocular rivalry is often characterized as a series of perceptual alternations between two competing images, the actual visual experience is more extensive and can be separated into three categories: (a) exclusive visibility, when one eye’s signal is entirely suppressed by the other eye’s image; (b) piecemeal mixed visibility in which information from both eyes is simultaneously visible in smaller spatially segregated areas, sometimes described as local rivalry (Skerswetat, Formankiewicz, & Waugh, 2017); and (c) superimposition mixed visibility in which information from both eyes is visible and combined to constitute a fused binocular percept (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Liu, Tyler, & Schor, 1992).

Importantly, mixed visibility highlights instances when complete interocular suppression fails, allowing binocular combination to occur. In fact, mixed visibility has been shown to be negatively associated with resting-state GABA levels in V1 (Freyberg, Robertson, & Baron-Cohen, 2015) and has likewise been shown to decrease after administration of GABA agonist drugs (Mentch, Spiegel, Ricciardi, Kanwisher, & Robertson, 2018). Disinhibition of interocular interactions are plausibly responsible for superimposition percepts, and piecemeal percepts are proposed to emerge from a weakening of the spatial coherence of these inhibitory interactions (Alais & Melcher, 2007; Kovacs, Papathomas, Yang, & Feher, 1996; Lee & Blake, 2004).

Our study on the effects of patching was inspired, in part, from the finding that the predominance of mixed visibility can be altered in real time by recent visual experience, we felt it would be pertinent to conduct a systematic investigation of patching-induced changes in rivalry dynamics using task instructions that require attending to mixed percepts.

To do so, we designed two experiments that permitted us to simultaneously quantify patching-induced changes in perceptual eye dominance and mixed visibility. Specifically, Experiment 1 utilized a novel rivalry task to quantify patching-induced changes in five different rivalry percept states: the exclusive percepts of the left and right eye’s images, the mixed percept biased in favor of the left and right eye’s images, and a balanced mixture of the left and right eye’s images. Our rationale for using this task design was to encourage participants not to classify mixed percepts biased in favor of one eye as an exclusive percept. This approach allowed us to more reliably estimate the relative predominance of mixed and exclusive visibility during rivalry while also allowing us to measure changes in perceptual eye dominance.

Experiment 2 was a follow up to Experiment 1 to determine whether piecemeal or superimposition percepts were specifically targeted by the effects of deprivation. To investigate this, we used a task adapted from Skerswetat et al. (2017) that allowed us to simultaneously measure patching-induced changes in perceptual eye dominance as well as the relative predominance of superimposition and piecemeal percepts.

Due to the findings that recent visual experience can alter binocular rivalry dynamics (Freyberg et al., 2015; Klink et al., 2010) and that monocular patching alters E-I balance in the visual cortex (Binda et al., 2017; Chadnova et al., 2017; Lunghi, Emir, et al., 2015), we predicted that patching would significantly increase the proportion and median duration of mixed percepts while simultaneously shifting perceptual eye dominance in favor of the deprived eye. Likewise, under the assumption that patching weakens interocular inhibition, we predicted that patching would selectively increase the proportion and median duration of superimposition rather than piecemeal percepts.
Experiment 1

We designed Experiment 1 to investigate the effects of short-term monocular patching on mixed visibility during rivalry. This experiment used a five-alternative, forced-choice (5AFC) binocular rivalry task to evaluate patching-induced changes in rivalry dynamics along a discretized spectrum of percept states that ranged from the exclusive percepts from the left eye’s image to that from the right eye’s image, including three intermediate mixed percept states.

Methods and materials

Observers

A total of 16 individuals enrolled in Experiment 1 (eight women, 22 ± 2.3, one author). Two participants were excluded from the study due to data-collection errors during baseline measurements, and one participant was excluded because the participant’s median rivalry phase durations at baseline were greater than 4 SD of the group mean. In sum, 13 individuals participated in the study. A subset of our participants (N = 5, three women, 24 ± 1.3) completed additional postdeprivation measurements that were taken over the course of an hour after removing the eye patch to evaluate the decay of the patching-induced changes in rivalry dynamics.

All participants had normal or corrected-to-normal visual acuity and were free from ocular diseases. Normal stereovision was confirmed through the Randot task. This research was approved by the ethics review board of the McGill University Health Center and was performed in accordance with the ethical standards laid down in the Code of Ethics of the World Medical Association (Declaration of Helsinki). Subjects gave written informed consent prior to the experiment. All participants except for the author YS were naive to the purpose of the experiment.

Apparatus

Each session took place in a quiet room with dim light. Visual stimuli for the binocular rivalry experiments were generated and controlled by an Apple MacBook Pro 2008 computer (MacOSX; Cupertino, CA) running MATLAB R2012B (MathWorks, Natick, MA) with the Psychtoolbox psychophysics toolbox (Brainard, 1997; Kleiner, Brainard & Pelli, 2007; Pelli, 1997). Stimuli were displayed on a wide 2300 3-D ready LED monitor ViewSonic V3D231, gamma corrected with a mean luminance of 100 cd/m². Subjects viewed the stimuli at a viewing distance of 70 cm with passive polarized 3-D glasses so that the left image was only seen by the left eye and the right image by the right eye.

The polarized filters had the effect of reducing the luminance to about 40%, measured with a photometer. The stereo image input was in top-down VGA format and was displayed in interleaved line stereo mode at a resolution of 1,920 × 1,080 p and a refresh rate of 60 Hz: the left-eye image was displayed in even scanlines, and the right-eye image was displayed in odd scanlines. Crosstalk levels for polarizing filter and passive goggle systems, such as the one we used are known to be low (luminance crosstalk: 1.14%, CI: [1.13, 1.15], contrast crosstalk: –0.04%, CI: [–0.28, 0.18]; Baker, Kaestner, & Gouws, 2016).

Stimulus

The dichoptic stimulus was composed of two orthogonal (±45°) sinusoidal gratings. These gratings were 3 c/°, subtending a diameter of 1.5° with a raised cosine annulus blurring the edges, Michelson contrast = 75%, presented inside a black-and-white noise pattern frame (side = 10°; Figure 1A).

Monocular deprivation

Using the Miles (1930) test for sensory eye dominance, we identified the dominant eye for each participant. We confirmed perceptual eye dominance with baseline binocular rivalry data for each subject (Dieter, Sy, & Blake, 2016) and proceeded to patch the nondominant eye for each experimental session in which they participated. We chose to patch the nondominant eye with the rationale that it has more capacity to increase its dominance; however, this claim has not yet been systematically evaluated. We used a diffuser eye patch that preserved most luminance information (40% luminance reduction) but eliminated all pattern information as confirmed by a Fourier decomposition of a natural image viewed through the patch. Although most studies use a patching duration of 2.5 hr, recent investigations have shown comparable effects after 2 hr of patching (Lunghi et al., 2016). To minimize the amount of time it would take to complete a single session, we monocularly deprived the nondominant eye for 2 hr.

Binocular rivalry task and experimental protocol

We designed the 5AFC binocular rivalry task used in Experiment 1 to extract more reliable information about rivalry dynamics than the conventional two (left vs. right) or three (left vs. mixed vs. right) AFC approach (Figure 1C). Reports of lower-than-expected levels of mixed visibility at baseline in other 2AFC or 3AFC rivalry studies (Lunghi et al., 2011) using similar stimulus parameters could be attributed to the fact that participants begin to miscategorize their rivalry per-
cepts, reporting a mixed percept biased in favor of one eye’s image as that eye’s exclusive percept. Our task design stresses attention to the phenomenological difference between mixed and exclusive percepts. An earlier article regarding the effect of stimulus parameters on the predominance of mixed visibility (O’Shea et al., 1997) was reported to be approximately 40% (SF: 3 c/°, field size: 1.5°). Our data set produced a similar figure with an average fraction of mixed visibility at baseline at 42% ± 5.76% (SEM).

At the beginning of each session, participants were told that they would see a dynamic stimulus during the experiment and that their task was to track what they were seeing with particular attention to timeliness and accuracy. Participants were given an illustration (Figure 1C) of the types of stimuli they would be seeing so as to better categorize their responses during the task.

Participants were instructed to continuously indicate whether they were seeing either (a) an exclusively left-tilted grating, (b) a mixed but predominantly left-tilted...
Computer work in a well-lit room. Normal activities, such as watching a movie or doing computer work in a well-lit room.

Subjects were instructed to keep both eyes open and do normal activities, such as watching a movie or doing computer work in a well-lit room.

The goal of preprocessing the raw rivalry time series data was to extract key features of the data usable for our analyses. Our main points of interest for analysis were patching-induced differences in (a) the median durations of the percept states, defined as the median of the distribution of durations spent perceiving each percept category; (b) the overall fraction of each percept state; and (c) perceptual eye dominance, defined as the ratio of the total durations spent viewing one eye’s exclusive percept versus the other’s.

The preprocessing pipeline consisted of four stages: (a) remove the first and last percept states in the time series as well as all percept states shorter than 250 ms to obtain the preprocessed time series, (b) extract the distribution of percept phase durations for each state from the processed time series, and (c) calculate the median and sum of these distributions to obtain the median and overall fraction of each of the states in each rivalry block.

Using this paradigm, we computed median phase durations as well as overall fractions for each of our five percept states (i.e., left, right, balanced mixed, mixed left, and mixed right; Figure 2B), allowing us to calculate ratios between the median phase durations of exclusive percepts (exclusive left vs. exclusive right) and mixed percepts (mixed left vs. mixed right). Although mean rivalry phase durations are used commonly in the literature to quantify perceptual dominance during rivalry (Blake & Logothetis, 2002; Klink et al., 2010; Lunghi et al., 2011; Sheynin et al., 2019; Zhou, Gao, White, Merk, & Yao, 2004), calculating the mean of the distribution is prone to be biased in favor of longer phase durations (Zhou et al., 2004); therefore, to account for this, we used the median rather than the mean of the phase duration distribution as a measure of perceptual dominance for each category.

Figure 2. Partitioning original rivalry data into different dependent variables. (A) Observer’s rivalry percept. (B) Ideal observer’s key press response corresponding to percept. (C) Obtaining phase durations of overall mixed visibility. We concatenated adjacent mixed percepts reported using the three mixed states in the original task to compute a new aggregated mixed percept state from which we extracted the median duration of mixed visibility.
In addition, our main measure of perceptual eye dominance was defined by

\[
\text{ODI} = \left(\frac{d_{\text{non-deprived}} - d_{\text{deprived}}}{d_{\text{non-deprived}} + d_{\text{deprived}}}\right),
\]

where the two \( d \) variables are the overall fractions for the exclusive percepts from the nondeprived and deprived eyes. This ratio computed a value between \(-1\) and \(1\), the extreme values indicating completely monocular vision from the nondeprived and deprived eyes, respectively. To evaluate deprivation-induced changes in these indices, we subtracted the baseline ratio from each postpatching ODI measure.

Importantly, our 5AFC design allowed us to repartition the three intermediate mixed percepts into a single variable: mixed visibility. This was achieved by concatenating adjacent mixed percepts in the original rivalry time series data (i.e., mixed left + balanced mixed + mixed right) to obtain a single mixed percept state. We then administered our preprocessing paradigm on this repartitioned time series to obtain distributions of phase durations for three percept states: exclusive left eye, mixed, and exclusive right eye (Figure 2C). We used the distribution corresponding to the repartitioned “mixed” category to calculate the overall fraction and median duration of mixed visibility.

To assess patching-induced effects across subjects and to account for intersubject variability at baseline, we calculated a value that represented the magnitude of the effect of patching on each dependent variable for each individual with respect to baseline. These values were obtained by dividing postpatching measures by those at baseline and then subtracting the normalized baseline. We conducted null hypothesis pairwise \( t \) tests on these normalized post/baseline values that determined whether deprivation significantly shifted the mean with respect to baseline (zero). We used the initial postdeprivation value for each dependent variable under the a priori assumption that the effect was maximal immediately after removing the patch. \( P \) values were corrected for multiple comparisons using the false discovery rate (FDR) correction method outlined in Benajmini and Hochberg (1995). We obtained 95% confidence intervals and the standard deviation of a distribution of 1,000 bootstrapped resamples (each drawing 13 subjects with replacement) of the normalized post/baseline values for each dependent variable. All SEMs in the current paper are equivalent to the standard deviation of the respective bootstrap distribution.

Further, we also conducted a one-way repeated-measures ANOVA on the postdeprivation measures from the subset of observers who completed additional rivalry blocks over the course of an hour after patching. This analysis, administered on normalized post/baseline values at 0, 30, and 60 min after patching, was used to establish the time course of the decay of the effects of patching. We compared the normalized post/baseline values across the three measured time points to determine the time course of the decay and then administered post hoc \( t \) tests to determine which time points were significantly shifted with respect to baseline.

Finally, we implemented a principal component analysis (PCA) to analyze the median duration data drawn from the reduced rivalry time series illustrated in Figure 2C. PCA is a statistical procedure that uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of values of uncorrelated variables called principal components (PCs). We observed that the median durations of the two exclusive percepts at baseline were highly correlated with one another (Spearman rho = 0.93, \( p < 0.0001 \)); therefore, a PCA transformation of the data would assist in mining statistically uncorrelated latent variables from the data that are arguably more informative of the neural processes underlying rivalry than the original task response variables used for analysis (Reynaud & Hess, 2017).

We used MATLAB’s built-in PCA function, specifying a singular value decomposition algorithm to extract the \( 3 \times 3 \) coefficient matrix of three PCs (three PCs explain 100% of the variance in a 3-D data set) from the baseline median duration data. We then used this coefficient matrix to project both the baseline and postpatching median duration data into the PC space defined at baseline using the procedure

\[
A_i = X_i \cdot C,
\]

where \( A_i \) is the representation of median duration data \( X_i \) at time point \( i \) (baseline or postpatching) in the PC space defined at baseline by the PC coefficient matrix \( C \). Both \( A_i \) and \( X_i \) are \( N \times 3 \) matrices, where \( N \) represents the total number of participants. The columns of \( X_i \) correspond to the median durations of the three percept categories (exclusive left, mixed, exclusive right), and the columns of \( A_i \) correspond to the PC scores for the three PCs extracted at baseline defined by coefficient matrix \( C \). We then conducted FDR-corrected pair-wise \( t \) tests on the postbaseline values for each PC column \( j \) in \( A_i \) (i.e., \( A_{ij} - A_{ij} \)) to evaluate patching-induced changes in the relative weight of each component’s influence on binocular rivalry dynamics with respect to baseline. Importantly, PCA does not rely on our a priori assumptions (and subsequent dependent variables of interest) of the underlying processes driving rivalry phase durations. On the contrary, PCA uncovers statistically uncorrelated components of rivalry phase-duration data that may then map onto our understanding of the neural mechanisms involved in binocular rivalry, allowing us.
to evaluate patching-induced changes within those components.

Results

We first analyzed the processed rivalry time series data to obtain median phase durations and overall fractions for each of our five percept states. We were interested to see how patching affected the fractions (Figure 3A) and median phase durations (Figure 3B) for the original five percept categories.

In contrast with previous findings (Lunghi et al., 2011), our results indicate that neither the fraction nor median duration of the deprived eye’s exclusive percept increase significantly after deprivation (fraction: \(M = 0.03, 95\% \text{ CI: } [-0.10, 0.16] \), FDR-corrected \(p < 0.05\); median duration: \(M = 0.06, 95\% \text{ CI: } [-0.05, 0.18] \), FDR-corrected \(p > 0.05\)). However, we do find that the fraction and median duration of the exclusive percept of the nondeprived eye decrease significantly: fraction, \(M = 0.31, 95\% \text{ CI: } [-0.41, -0.20] \), \(t(12) = -5.41, \text{ FDR-corrected } p < 0.001\); median duration, \(M = 0.15, 95\% \text{ CI: } [-0.24, -0.04] \), \(t(12) = -2.91, \text{ FDR-corrected } p < 0.05\). This implies that the shift in perceptual eye
dominance observed after patching may be driven by a
decrease in the input strength of the nondeprived eye’s
image rather than a reciprocal increase in the deprived
eye’s contribution.

Further, the median duration of the mixed percepts
biased in favor of the nondeprived eye’s image
increased significantly after patching, mean difference =
0.30, 95% CI: [0.17, 0.46], t(12) = -4.09, FDR-corrected
p < 0.01, as did that of the deprived eye’s image, mean
difference = 0.28, 95% CI: [0.09, 0.51], FDR-corrected p
> 0.05. Increases in the overall fractions of all three
mixed percepts were also observed: fraction mixed
(nondeprived eye), M = 0.46, 95% CI: [0.15, 0.89], t(12)
= 3.19, FDR-corrected p < 0.05; fraction mixed
(balanced), M = 0.72, 95% CI: [0.11, 1.55], FDR-
corrected p > 0.05; fraction mixed (deprived eye), M =
0.47, 95% CI: [0.21, 0.75], t(12) = 3.19, FDR-corrected p
< 0.05. These results indicate that the mixed percepts
were enhanced without the introduction of eye-specific
bias.

To further investigate, we analyzed changes in the
overall fraction (Figure 4A) and median duration
(Figure 4B) of overall mixed visibility (extracted from
the reduced time series illustrated in Figure 2C).
Patchig significantly increased both the overall fraction
of mixed visibility, Figure 4A, M = 0.33,
bootstraped 95% CI: [0.19, 0.52], t(12) = 3.51, FDR-
corrected p < 0.01, and the median duration of mixed
visibility, Figure 4B, M = 0.30, bootstraped 95% CI:
[0.17, 0.44], t(12) = 4.17, FDR-corrected p < 0.01. The
shift in perceptual eye dominance (using the exclusive
percepts) was also highly significant, M = 0.20, 95% CI:
[0.11, 0.29], t(12) = 4.42, p < 0.001, Figure 4C.
Interestingly, we did not observe a significant shift in
perceptual eye dominance within the mixed percepts, mean
difference = 0.03, 95% CI: [-0.04, 0.11], t(13) =
0.78, p > 0.05, further suggesting that the shift in
perceptual eye dominance and the increase in mixed
visibility may be separate effects of patching.

For five out of the 13 participants, we collected data
from rivalry blocks at 0, 30, and 60 min after patching
to determine the time course of the decay of the
patching-induced effects. We conducted repeated-meas-
ures ANOVAs on the group means for the three
postdeprivation measurements to evaluate whether the
patching-induced shifts changed significantly over the
course of the experiment. Due to the small number of
participants in this subset, most of our statistical tests
for these analyses were underpowered. They still,
however, give a noteworthy insight into both the
intersubject variability of these effects and their time
courses over an hour after patching.

The ANOVA did not yield a significant decay of the
effect of MD on the overall fraction of mixed visibility
(which was weak to begin with in this smaller
subsample), Wilks’ lambda = 0.60, F(2, 10) = 1.30, p <
0.05, \eta^2_p = 0.21, (Figure 4A, right panel). However,
there was an observable trend of recovery to baseline
levels over the course of an hour after patching (t0: M =
0.74, 95% CI: [-0.22, 1.71]; t30: M = 0.65, 95% CI:
[0.06, 1.23]; t60: M = 0.31, 95% CI: [-0.37, 0.99]).
Likewise, the ANOVA did not produce a significant
decay of the effect of MD on the median duration of
mixed visibility, Wilks’ lambda = 0.60, F(2, 8) = 1.55, p
> 0.05, \eta^2_p = 0.28 (Figure 4B); however, there was also an
observable trend of recovery to baseline levels over
the course of an hour after patching (t0: M = 1.18, 95% CI:
[0.06, 2.30]; t30: M = 0.64, 95% CI: [-0.43, 1.74];
t60: M = 0.28, 95% CI: [-0.55, 1.13]).

Finally, the decay of the effect of MD on perceptual
eye dominance was also not significant for this subset
of participants, Wilks’ lambda = 0.27, F(2, 8) = 1.78, p
> 0.05, \eta^2_p = 0.30 (Figure 4C, right panel). However,
perceptual eye dominance was significantly shifted with
respect to baseline immediately following MD, M =
0.12, 95% CI: [0.10, 0.23], t(4) = 3.1, FDR-corrected p
< 0.05), as well at 30 min after removing the patch, M =
0.08, 95% CI: [0.05, 0.11], t(4) = 7.37, FDR-corrected p
< 0.01, but not at 60 min (FDR-corrected p > 0.05),
suggesting a gradual recovery to baseline levels.

Our initial analyses found that the median durations of
the two exclusive percepts are highly correlated with
one another (Spearman rho = 0.93, p < 0.001). This
finding inspired us to utilize a PCA to transform the
variables in our median duration data set (exclusive
left, mixed, exclusive right) into a new set of statistically
uncorrelated variables that were possibly more inform-
ative of neural processes underlying rivalry. We
administered a descriptive PCA on the baseline median
durations extracted from the processed time series
illustrated in Figure 2C to uncover three PCs that
explained 100% of the variability in our data (Figure
5A). The PCA coefficients indicate the degree to which
each PC (PCs 1–3) is associated with the original rivalry
percept variables. PC 1 is most closely associated with
the median duration of mixed visibility and explains
70.10% of the variability in the baseline data. For the
purpose of this analysis, PC 1 can be interpreted as the
binocular combination component underlying rivalry
phase durations. For PC 2, the PCA extracted the
correlation between the two exclusive percept variables;
PC 2 is most closely associated with the median
duration of both exclusive percepts and explains
28.94% of variability in the data. PC 2 can then be
feasibly regarded as the perceptual suppression com-
ponent underlying rivalry phase durations. Finally, PC
3 is anticorrelated between the two exclusive percepts
and uncorrelated with mixed visibility; this PC explains
the remaining 0.95% of the variability in the data. PC 3
points to interocular balance, or perceptual eye
dominance, as a small underlying component influ-
encing the baseline rivalry phase duration data.
We transformed both the baseline median duration data and the postpatching median duration data by projecting these data sets into the PC space defined by the coefficient matrix extracted from the baseline data. This procedure yielded two data sets, corresponding to the PC scores for each participant for each PC before and after monocular patching (see “Methods” for more details). As a sanity check, we confirmed correlations...
between these PC scores and the features they represented in the baseline data. For PC 1, this was the median duration of mixed visibility; for PC 2, this was the median duration of exclusive visibility (the arithmetic mean of the median durations of the two exclusive percepts); and for PC 3, this was perceptual eye dominance, calculated using the procedure outlined in Equation 1. We z-normalized (mean = 0, standard deviation = 1) both the PC scores and their corresponding features in the original data set to ensure both sets were scaled similarly for comparison. The PC scores were all significantly correlated with the features we extracted from the original data set, $F(1, 12) \geq 21.4, ps < 0.001, \text{adjusted } R^2 \geq 0.61$, indicating the PCA successfully extracted meaningful components underlying the phase-duration data at baseline (Figure 5C).

FDR-corrected pair-wise $t$ tests were conducted on the postbaseline PC scores. We found that patching significantly increased the mean score of PC 1, $M = 0.65, 95\% \text{ CI: [0.09, 1.21]}, t(13) = 2.52, \text{FDR-corrected } p < 0.05$, and PC 3, $M = 0.33, 95\% \text{ CI: [0.11, 0.55]}, t(13)$

Figure 5. PCA on median rivalry phase duration data. (A) Output of the PCA. The PCA was administered on baseline rivalry phase durations drawn from the reduced processed time series illustrated in Figure 2C. The components are statistically uncorrelated, pointing to three unique processes underlying the phase-duration data. The PCA coefficients indicate the degree to which each principal component (PCs 1–3) is associated with the median durations of each percept type. PC 1 is most closely associated with the median duration of mixed visibility, PC 2 is most closely associated with the median duration of complete perceptual suppression, and PC 3 is plausibly interpreted as ocular imbalance or perceptual eye dominance (see Methods for more information on the PCA). (B) Correlating baseline PCA scores with baseline binocular rivalry features. The $x$-axis corresponds to the z-normalized PC scores for each PC across subjects; the $y$-axis values indicate z-normalized values corresponding to the following baseline median phase duration data: PC 1, median duration of mixed visibility; PC 2, median duration of exclusive visibility (the arithmetic mean of the exclusive percepts’ median durations); and PC 3, the ratio of the median durations of the exclusive percepts defined in Equation 1. PC scores are highly correlated with their respective binocular rivalry features. (C) Comparing postbaseline PC scores. Pre- and postpatching PC scores were obtained using the method outlined in Methods. PC scores indicate the degree to which each PC weighs on an individual’s rivalry data. Each bar indicates the group $M \pm \text{ SEM}$. See panel C for corresponding information. Asterisks indicate significant interactions. *FDR-corrected $p < 0.05$. 

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3.31, FDR-corrected \( p < 0.05 \), but not PC 2, \( M = -0.06 \), 95% CI: \([-0.44, 0.30]\), \( t(13) = -0.40 \); FDR-corrected \( p > 0.05 \). Notably, the PCA uncovered statistically uncorrelated components of rivalry phase duration data that map on quite well to our understanding of several factors involved in binocular rivalry: binocular combination, perceptual suppression, and perceptual eye dominance. This approach allowed us to evaluate patching-induced changes within these mechanistic components, extending the insights of the previous analyses. Specifically, our results indicate that MD affects putative neural mechanisms responsible for binocular combination and perceptual eye dominance rather than those responsible for exclusive dominance.

### Experiment 2

We designed Experiment 2 to investigate whether short-term monocular patching preferentially affects superimposition versus piecemeal mixed percepts during binocular rivalry. This experiment used a 4AFC binocular rivalry task adapted from Skerswetat et al. (2017) to evaluate patching-induced changes in rivalry dynamics.

### Methods and materials

#### Observers

A total of 11 individuals enrolled in Experiment 2 (eight women, 21, \( \pm 2.1 \), one author). One participant was excluded from the study due to a failure to complete the full experiment; therefore, in sum, 10 individuals participated the study. Two participants completed both Experiments 1 and 2.

#### Apparatus

Each session took place in a quiet room with dim light. The original display system we used in Experiment 1 was not available at the time of data collection for Experiment 2; therefore, stimuli were displayed on the Oculus DK2 VR headset to dichoptically present the binocular rivalry stimuli generated and controlled by the same computer system as described in Experiment 1. The Oculus was gamma-corrected with a mean luminance of 90 cd/m², driven at a resolution of 960 \( \times \) 1,080 per eye, with a refresh rate of 60 Hz and a nominal field of view of 100°. The left- and right-eye images were separated by a divider such that the left eye only viewed the left side of the goggles and the right eye only viewed the right side.

#### Stimulus

The dichoptic stimulus used in Experiment 2 was identical to that of Experiment 1 with the exception that we used a larger stimulus (4 c/°), subtending a diameter of 2° with a raised cosine annulus blurring the edges, Michelson contrast = 80%) due to the pixel density limitations of the Oculus DK2 headset.

#### Binocular rivalry task and experimental protocol

We adapted a 4AFC binocular rivalry task used by Skerswetat et al. (2017; Figure 1D) to quantify the overall fraction of exclusive, piecemeal, and superimposition mixed percepts. At the beginning of each session, participants were shown images on a document that illustrated the differences between the left-oriented, right-oriented, and superimposition versus piecemeal mixed percepts. Participants were told that they would see a dynamic stimulus during the experiment and that their task was to track what they were seeing with particular attention to timeliness and accuracy. Aside from the response criteria, all other aspects of the stimulus and task were identical to that described for Experiment 1.

Participants were given the option to continuously indicate whether they were seeing either (a) an exclusively left-tilted grating, (b) an exclusively right-tilted grating, (c) a superimposition mixed percept, or (d) a piecemeal mixed percept. Participants used three adjacent keys for the task, using the left to indicate exclusive left tilt, right for right tilt, holding down a combination of the left and right keys for the piecemeal percepts, and the middle key for the superimposition percepts. In our instructions, we specified that exclusive percepts were those with 90% or more left- or right-tilted lines, and the mixed percepts were between 50% and 90% left- or right-tilted lines. Postdeprivation assessments were administered at 0, 15, 30, and 60 min after patching.

#### Preprocessing and Statistical Analysis

We used the same preprocessing paradigm described in Experiment 1; however, we also developed an additional dependent variable to investigate postbaseline differences in the mixed perceive ratio (MPR) defined by the following equation:

\[
\text{MPR} = \frac{d_{\text{superimposition}} - d_{\text{piecemeal}}}{d_{\text{superimposition}} + d_{\text{piecemeal}}},
\]

where the two \( d \) variables indicate the overall fraction reported for seeing superimposition and piecemeal percepts, respectively. Negative values in the MPR indicated bias in favor of superimposition percepts, and positive values indicated bias in favor of piecemeal percepts.

\[\text{MPR} \approx \frac{\text{superimposition perceptions}}{\text{piecemeal perceptions}}, \]

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percepts. Patching-induced changes in the MPR were obtained by subtracting baseline from postpatching values.

We conducted pairwise t tests on the first postpatching measurement and baseline for (a) the overall fraction of mixed visibility, (b) the median duration of mixed visibility, (c) the mixed percept ratio (MPR), and (d) the eye dominance index (ODI). We also conducted a repeated-measures ANOVA with complementary post hoc paired t tests on the MPR and ODI values to determine the time course of the decay of the effect of patching on these variables.

Results

We first wanted to see if the results observed in Experiment 1 were also measurable using a binocular rivalry task with different response instructions. Using this rivalry task, we replicated the finding that 2 hr of MD increases both the fraction, \( M = 1.09, 95\% \text{ CI: } [0.24, 1.93], t(9) = 2.98, p < 0.05 \), and median duration, \( M = 0.24, 95\% \text{ CI: } [0.04, 0.43], t(9) = 2.74, p < 0.05 \), of mixed visibility during rivalry. Perceptual eye dominance was also significantly shifted in favor of the deprived eye with respect to baseline, \( M = 0.12, 95\% \text{ CI: } [0.01, 0.23], t(9) = 2.52, p < 0.05 \).

Furthermore, we also found that the MPR shifts significantly in favor of superimposition immediately after MD, \( M = -0.25, 95\% \text{ CI: } [-0.62, -0.12], t(9) = -2.75, p < 0.05 \). This indicates that the increase in mixed visibility observed in this experiment and in Experiment 1 is likely due to increases in the superimposition percepts rather than piecemeal percepts. This was confirmed by separate paired t tests on the normalized postbaseline fractions for both superimposition and piecemeal percepts immediately after deprivation: superimposition, \( M = 0.08, 95\% \text{ CI: } [0.03, 0.12], t(9) = 4.01, \text{ FDR-corrected } p < 0.01 \); piecemeal, \( M = -0.02, 95\% \text{ CI: } [-0.07, 0.02], t(9) = -1.06, \text{ FDR-corrected } p > 0.05 \).

To determine the time course of this effect of deprivation, we also conducted repeated-measures ANOVAs on the change in the overall fraction of mixed visibility, the shift in the MPR (Figure 6A), and the shift in perceptual eye dominance (Figure 6B) across four postdeprivation time points at 0, 15, 30, and 60 min after removing the patch.

The decay of the effect of MD on perceptual eye dominance across these four time points was not significant for these observers, Wilks’ lambda = 0.47, \( F(3, 27) = 0.38, p > 0.05, \eta^2_p = 0.13 \) (Figure 6B). However, the perceptual eye dominance shift was significant immediately after removing the eye patch and remained significant until 30 min after removing the patch, \( t(9) > 2.98, \text{ FDR-corrected } ps < 0.05 \).

Likewise, the decay of the effect of MD on the overall fraction of mixed visibility across the five time points was also not significant, Wilks’ lambda = 0.39, \( F(3, 27) = 1.30, p > 0.05, \eta^2_p = 0.13 \) (Figure 6A). However, the magnitude of the effect of MD on the fraction of mixed visibility was greatest directly following MD, \( M = 0.31, 95\% \text{ CI: } [0.06, 0.56], t(9) = 2.8, \text{ FDR-corrected } p < 0.05 \), as well as at 15 min after

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**Figure 6.** Experiment 2: Patching-induced changes in superimposition versus piecemeal mixed visibility during rivalry. (A) Decay of patching-induced effect on fraction mixed visibility and MPR. The overall fraction of mixed visibility (red + green) is the sum of the absolute predominance of superimposition percepts (shown in green) and that of the piecemeal percepts (shown in red). The top rows of asterisked interactions indicate a significant increase in the fraction of mixed visibility at t0 and t15 with respect to baseline. The bottom row of asterisked interactions indicates an increase in the absolute predominance of superimposition percepts at t0, t15, and t60 with respect to baseline. Piecemeal percepts did not shift significantly with respect to baseline. (B) Decay of patching-induced effect on perceptual eye dominance. Perceptual eye dominance gradually recovers to baseline. Asterisks indicate significant differences with respect to baseline. * \( p < 0.05 \).
removing the patch, $M = 0.30$, 95% CI: [0.15, 0.45], $t(9) = 4.65$, FDR-corrected $p < 0.01$.

Similarly, the decay effect of the effect of MD on the MPR was also not significant, Wilks’ lambda $= 0.63$, $F(3, 27) = 0.70$, $p > 0.05$, $\eta^2_p = 0.07$ (Figure 6A), suggesting the ratio of superimposition to piecemeal percepts did not change significantly over the course of our postdeprivation measurements. The MPR did, however, shift significantly in favor of superimposition with respect to baseline across three out of four of our measure time points: 0, 15, and up to at least 60 min after MD, $t(9) > 2.98$, FDR-corrected $ps < 0.05$.

**Discussion**

We conducted two experiments to characterize the effects of short-term monocular patching on the occurrence of mixed percepts during binocular rivalry. Our investigation was inspired by recent findings that patching alters E-I balance in visual cortex (Binda et al., 2017; Chadnova et al., 2017; Lunghi, Emir, et al., 2015) and that the absolute predominance of mixed visibility during rivalry can be modified through recent visual experience (Klink et al., 2010; Said & Heeger, 2013) as well as with neuromodulators (Mentch et al., 2017).

Experiment 1 utilized a rivalry task that enabled us to accurately quantify patching-induced changes in perceptual eye dominance as well as in the overall fraction and median duration of mixed visibility during rivalry. Our results from this experiment demonstrated that patching causes enhancements in both the fraction and median duration of mixed visibility during rivalry. Further, our data also suggest that patching achieves a perceptual eye dominance shift in favor of the deprived eye by reducing the overall predominance and median duration of the nondeprived eye’s image while simultaneously reallocating its responses among the mixed percepts.

This finding contrasts with previous rivalry studies on patching that found the shift in perceptual dominance is caused by an increase in the strength of the deprived eye and a reciprocal decrease in the nondeprived eye (Lunghi et al., 2011; Lunghi et al., 2019; Lunghi, Emir, et al., 2015). It is important to note, however, that the conclusions drawn from our data are not entirely in disagreement with these previous results because the previous studies monocularly deprived the dominant eye and our study always deprived the nondominant eye. This distinction is possibly related to Levelt’s proposition II (Levelt, 1965) or, more appropriately, modified proposition II (Brascamp, Klink, & Levelt, 2015), which states that, when the input strength of the two eyes are independently altered, the dominance duration of the eye with the stronger input is maximally affected. In the context of our study, it is reasonable to consider the nondeprived (dominant) eye as the eye with the stronger input at baseline. It is, therefore, plausible that patching-induced changes in the signal strength of the deprived eye would preferentially affect the dominance duration of the nondeprived eye as we observe in our results.

Our study also demonstrated that perceptual eye dominance shifts within the exclusive percepts while the two biased mixed-percept categories increase independently of eye of origin. This finding presents the possibility that deprivation impacts exclusive dominance and mixtures differently. It is possible, however, that our participants did not accurately classify the three fractional mixed percept categories because they alternated faster and were more difficult to keep track of than the exclusive percepts. Although our task design sought to ensure that participants do not miscategorize “biased” mixed percepts as exclusive percepts, it also introduced a possible source of error in the categorization of the three mixed-percept categories. For this reason, it may be fruitful for future studies utilizing our task to employ a “replay” rivalry control condition to evaluate possible criterion effects latent in the task. Relatedly, an unpublished experiment conducted by the authors demonstrated that 5 min of monocular deprivation did not change the response criterion for mixed visibility during replay rivalry (although it did shift perceptual eye dominance and also enhance mixed visibility in normal rivalry). Our approach to circumnavigate this issue in the present study, however, was to implement a PCA that aimed to transform the original data into statistically uncorrelated components underlying rivalry phase durations that were invariant to eye of origin. Using this approach, we identified three components that corresponded to several hypothesized mechanisms involved in producing the rivalry states: (a) binocular combination, (b) perceptual suppression (agnostic to eye of origin), and (c) perceptual eye dominance. This approach, which has previously been used to infer neural mechanisms from behavioral data (Reynaud & Hess, 2017), offered additional evidence for the idea that MD has two identifiable and statistically distinguishable effects on binocular rivalry dynamics: (a) an increase in ocular imbalance and (b) an increase in binocular combination.

The main conclusions drawn from Experiment 1 can be plausibly understood by the idea that MD achieves its effects by weakening interocular inhibition. We designed Experiment 2 to assess this idea. We adapted a rivalry task previously developed by Skerswatet et al. (2017) to investigate patching-induced changes in the relative predominance of superimposition and piecemeal mixed percepts. Whereas superimposition per-
cepts can be thought of as fully fused binocular percepts, the result of weakened interocular suppression, piecemeal percepts can be considered to be intermediary binocular percepts, in which rivalry is still occurring in smaller subregions (Alais & Melcher, 2007; Klink et al., 2010; Kovacs et al., 1996; Lee & Blake, 2004). Superimposition and piecemeal mixed percepts have been previously attributed to arise from two different but related aspects of interocular inhibition: gain and spatial coherence, respectively (Klink et al., 2010). Superimposition percepts would then indicate a reduction in the overall gain of interocular inhibition while piecemeal perception points to reduced spatial coherence of interocular inhibition. The finding that patching enhances the relative predominance of superimposition percepts, although not significantly affecting piecemeal visibility, adds complementary evidence to the idea that MD attenuates the gain of interocular inhibitory interactions.

It is also noteworthy to add that superimposition percepts during binocular rivalry are known to appear infrequently with the stimulus parameters used in our study (Hollins, 1980), and when they are visible, the component gratings often do not appear equal in clarity and contrast (Yang, Rose, & Blake, 1992). Assuming the neural mechanisms underlying superimposed visibility immediately after patching are the same ones promoting those states at baseline, the significant increase in superimposition visibility implicates patching as a potent method to reduce interocular inhibition. In this way, our results are related to previous investigations evaluating the role of inhibitory interocular interactions in rivalry, in which prolonged exposure to rivalrous binocular stimuli also causes an increase in superimposed mixed visibility (Klink et al., 2010; Said & Heeger, 2013).

Although the effects of short-term patching on perceptual eye dominance are well documented (Baldwin & Hess, 2018; Kim et al., 2017; Lunghi, Berchicci, et al., 2015; Lunghi et al., 2011; Zhou, Clavagnier, & Hess, 2013), the current study presents the first evidence that monocular patching also enhances binocular combination. Previous studies using binocular rivalry with similar stimulus parameters to assess the effects of monocular patching (Lunghi et al., 2011; Lunghi et al., 2019; Lunghi, Emir, et al., 2015) excluded participants with greater than 20% overall predominance of mixed visibility at baseline. Although such exclusion criteria may improve accuracy in measures of perceptual eye dominance, it also reduces the generalizability of these results to the overall population, in which the average proportion of mixed visibility using the stimulus parameters mentioned in our paper ranges between 30% and 60% (O’Shea et al., 1997).

Theoretical implications

Importantly, our main findings are compatible with several proposed computational frameworks of binocular rivalry. For instance, the patching-induced increase in mixed visibility aligns well with the work done by Brascamp et al. (2013). In this paper, the authors present an experimentally derived model of rivalry in which eye-specific neural events in early processing areas contribute to perceptual competition during stimulus rivalry (in which incongruent images are continuously swapped between the two eyes but representations of the images rival as in binocular rivalry). As patching likely causes changes in early eye-specific cortical areas (Chadnova et al., 2017; Lunghi, Emir, et al., 2015; Tso et al., 2017), our data contribute to the idea that changes in monocular neural activity can modulate the resolution of binocular rivalry. This model contrasts with other computational approaches to binocular rivalry that attribute perceptual competition to exclusively higher-order binocular areas (Wilson, 2003). An interesting avenue of future study will be to investigate whether patching also affects perceptual eye dominance and mixed visibility during stimulus rivalry. Such work can further reveal the neural loci of the two identifiable effects of monocular patching on rivalry dynamics mentioned in the current study.

Likewise, the finding that patching enhances binocular combination is compatible with computational frameworks of rivalry that include opponency neurons (Blake, 1989; Li, Rankin, Riznel, Carrasco, & Heeger, 2017; Said & Heeger, 2013). Opponency neurons, or XOR neurons, detect interocular conflict and play a role in the resolution of binocular rivalry. In the Said and Heeger (2013) model of binocular rivalry, opponency neurons inhibit preceding feed-forward units such that an adaptive reduction in the activity of these inhibitory interneurons results in a facilitation of binocular combination. This model succeeds at predicting experimental evidence in which adaptation to interocular flicker of left- and right-oriented monocular gratings (targeting opponency neurons) subsequently produces more mixed visibility during rivalry than a binocular adaptor of the same stimuli (not targeting opponency neurons). Similarly, in our case, temporarily depriving one eye of input can be conceived of as (a) preferentially adapting binocular opponency neurons and also (b) adapting the feed-forward monocular signal of the nondeprived eye. Removing the eye patch subsequently causes a relative enhancement in (a) the perception of mixtures and (b) a shift in balance in favor of the deprived eye. It is worth mentioning that recent physiological evidence has identified populations of neurons that are synchronized with the intermodulation of monocular SSVEP signals during rivalry (Katyal, Engel, He, & He, 2016) in line with these
theoretical insights (Blake, 1989; Li et al., 2017; Said & Heeger, 2013).

Finally, it is feasible to consider that the two effects of MD on binocular rivalry dynamics discussed in this article emerge, in part, as a result of the type of attentional gain mechanism described in Li et al. (2017). Attention is a well-established factor influencing binocular rivalry dynamics (see Carrasco, 2011; Dieter & Tadin, 2011; Dieter, Brascamp, Tadin, & Blake, 2016). In their model, Li et al. (2017) propose that attentional modulation from higher-order visual areas amplifies perceptual competition by biasing attentional gain to one of the rival stimuli. According to the model, prolonged adaptation of such an attentional mechanism would subsequently result in a decrease of perceptual suppression during rivalry. A patching-induced adaptation of this type of attentional mechanism could account for the reduction of perceptual exclusivity we observe in our experiments. Taking this possibility a step further, our findings may contribute new evidence for the existence of eye-specific attentional channels (Saban, Sekely, Klein, & Gabay, 2018; Self & Roelfsema, 2010), in which adaptation of the nondeprived eye’s attentional channel subsequently shifts perceptual balance in favor of the deprived eye.

**Conclusion**

In summary, our study provides new insights on the effects of short-term adult MD. Although we have known for some time that patching causes a temporary shift in perceptual eye dominance, we now know that some of this shift is attributed to a reallocation of responses toward the perception of mixtures. The findings of the present study contribute to the growing evidence that short-term MD causes a temporary functional plasticity observable at the level of E-I balance in early visual cortex. It will be beneficial for future rivalry studies on MD to take advantage of a detailed account of the intermediary mixed percepts to further advance our knowledge of the underlying brain mechanisms and to sharpen our understanding of binocular visual plasticity in general.

**Keywords:** neuroplasticity, E-I balance, mixed percepts, binocular rivalry, short-term monocular deprivation

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Commercial relationships: none.
Corresponding author: Yasha Sheynin. Email: jacob.sheynin@mail.mcgill.ca.
Address: McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montréal, QC, Canada.

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