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Article *in* European Journal of Neuroscience · September 2020

DOI: 10.1111/ejn.14971

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Received: 28 May 2020 | Revised: 27 August 2020 | Accepted: 2 September 2020

DOI: 10.1111/ejn.14971

RESEARCH REPORT

EJN European Journal of Neuroscience FENS WILEY

Modulation of binocular rivalry with rapid monocular visual stimulation

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Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPAS-477166 and RPIN-05394; Canadian Foundation for Innovation, Grant/Award Number: 34095

Abstract

Rapid visual stimulation can increase synaptic efficacy by repeated synaptic activation. This long-term potentiation-like (LTP-like) effect can induce increased excitability in the human visual cortex. To examine the effect of rapid visual stimulation on perception, we tested the hypothesis that rapid monocular visual stimulation would increase the dominance of the stimulated eye in a binocular rivalry task. Participants ($n = 25$) viewed orthogonal 0.5 cpd gratings presented in a dichoptic anaglyph to induce binocular rivalry. Rivalry dynamics (alternation rate, dominance, and piecemeal durations) were recorded before and after 2 min of rapid monocular stimulation (9 Hz flicker of one grating) or a binocular control condition (9 Hz alternation of the orthogonal gratings viewed binocularly). Rapid monocular stimulation did not affect alternation rates or piecemeal percept duration. Unexpectedly, the rivalry dominance of the stimulated eye was significantly reduced. A further experiment revealed that this effect could not be explained by monocular adaptation. Together, the results suggest that rapid monocular stimulation boosts dominance in the non-stimulated eye, possibly by activating homeostatic interocular gain control mechanisms.

KEYWORDS

binocular rivalry, long-term potentiation, neuroplasticity, ocular dominance, visual tetanus

1 | INTRODUCTION

Long-term potentiation (LTP) is the process of strengthening synaptic efficacy through repeated activation. This fundamental mechanism of neuroplasticity involves a cascade of cellular and molecular changes and underpins the processes of learning and memory formation (Bliss & Collingridge, 1993; Bliss & Lomo, 1973). Early research revealed that the rapid electrical stimulation of presynaptic cells within the rabbit hippocampus induced a lasting increase in the response amplitude of postsynaptic cells (Bliss & Lomo, 1973). Subsequent studies demonstrated similar effects (Bröcher et al., 1992) and characterized the neurochemical changes that occurred as a result of the stimulation (Hayashi et al., 2000; Teyler & DiScenna, 1987). These changes included a rise in postsynaptic calcium, the release of glutamate, and the activation of *N*-methyl-D-aspartate (NMDA) receptors (Malenka & Nicoll, 1999). While LTP is typically induced using electrical stimulation in vitro, similar effects (a strengthening of neural responses following stimulation) have been reported in the visual

Abbreviations: LTD, long term depression; LTP, long term potentiation; NMDA, N-methyl-d -aspartate; VEP, visual evoked potentials.

Edited by: Dr. Guillaume Rousselet

cortex using rapid visual stimulation in adult rats (Frenkel et al., 2006; Heynen & Bear, 2001) and in humans (Clapp et al., 2005; Normann et al., 2007; Teyler et al., 2005).

In human adults, 2-min of rapid visual stimulation using a high-contrast checkerboard increased the amplitude of the N1b component of visual evoked potentials (VEPs; Normann et al., 2007; Sanders et al., 2018; Teyler et al., 2005). Rapid visual stimulation, sometimes referred to as visual tetanus, has been delivered in a number of ways including 9 Hz flicker of checkerboard or grating stimuli and 2 Hz pattern reversal of checkerboard stimuli (Normann et al., 2007; Teyler et al., 2005). To account for the effect of visual adaptation that can reduce visual cortex excitability and VEP amplitude (Blakemore & Campbell, 1969), most studies of rapid visual stimulation include a period of eye closure that at least matches the duration of rapid visual stimulation (Magnussen & Greenlee, 1985). The effect of rapid visual stimulation on VEP amplitude is stimulus-specific (Ross et al., 2008; Vassilev et al., 1994), reliant on NMDA receptors in animal models (Clapp et al., 2006), and may also involve an increase in glutamate receptor expression (Eckert et al., 2013), suggesting that it involves an LTP-like mechanism.

The majority of studies on rapid visual stimulation in humans have used electrophysiology or neuroimaging to measure visual cortex excitability before and after stimulation (Sanders et al., 2018). Therefore, the perceptual effects of rapid visual stimulation, if any, are not well understood. This is an important issue. If the LTP-like changes in cortical excitability induced by rapid visual stimulation can modulate perception, rapid visual stimulation may have therapeutic applications. For example, repetitive transcranial magnetic stimulation of the visual cortex can transiently improve visual functions such as contrast sensitivity in adults with amblyopia, a neurodevelopmental disorder of vision (Clavagnier et al., 2013; Thompson et al., 2008; Tuna et al., 2020). Like rapid visual stimulation, the effects of repetitive transcranial magnetic stimulation on cortical excitability likely involve LTP-like mechanisms (Hoogendam et al., 2010). Therefore, rapid visual stimulation may have similar effects and, unlike repetitive transcranial magnetic stimulation, can be delivered to the thalamocortical inputs from just one eye. This property may make repetitive visual stimulation particularly well suited for the treatment of amblyopia, which is characterized by a large imbalance in the neural response generated by each eye (Barnes et al., 2001).

Two preliminary studies have reported behavioral effects of rapid visual stimulation. Beste et al. observed improved luminance discrimination following 40 min of 20 Hz rapid visual stimulation, whereas Clapp et al. observed a reaction time improvement, but no change in response accuracy, during a checkerboard detection task following 2 min of 9 Hz stimulation (Beste et al., 2011; Clapp et al., 2012). In this experiment, we further explore the behavioral effects of rapid visual stimulation by investigating the effect of monocular rapid visual stimulation on binocular rivalry.

Binocular rivalry is a form of bistable perception wherein conflicting monocular images stochastically compete for dominance when viewed dichoptically. The resulting percept can involve periods of complete perceptual dominance by one eye, and periods of a mixed, piecemeal percept whereby images are superimposed or each eye dominates in different regions of the visual field (Wilson et al., 2001). In individuals with normal binocular vision, the periods of perceptual dominance are relatively equal between the two eyes. However, the relative dominance of each eye during binocular rivalry can be modulated by presenting stimuli with features such as size (Kang, 2009), color (Stalmeier & de Weert, 1988), luminance (Hong & Shevell, 2008), orientation (Holmes et al., 2006), or spatial frequency (Fahle, 1982), that differ between the two eyes.

In this study, we induced binocular rivalry by dichoptically presenting orthogonal, sinusoidal gratings. Dichoptic presentation was achieved using red/green anaglyphs. The aim of our first experiment was to determine suitable grating parameters. Specifically, we aimed to identify a stimulus configuration that generated minimal time spent in piecemeal and stable alternation rates across trials. In our second experiment, we used this stimulus to assess whether monocular rapid visual stimulation modulates binocular rivalry dynamics and/or dominance durations in individuals with normal binocular vision, based on previous work showing that rapid visual stimulation induces LTP-like effects in the human visual cortex (Clapp, et al., 2006; Normann et al., 2007; Ross et al., 2008; Sanders et al., 2018; Teyler et al., 2005). Our hypothesis was that rapid monocular visual stimulation would strengthen the cortical response to inputs from the stimulated eye and that this would increase the relative time spent perceiving the stimulus presented to the stimulated eye during binocular rivalry (i.e. increase the perceptual dominance of the stimulated eye). In a third experiment, we measured binocular rivalry before and after viewing a monocular static grating as a test of monocular visual adaptation.

2 | MATERIALS AND METHODS

Three experiments were performed. Experiment 1 investigated the parameters for the binocular rivalry stimulus. Experiment 2 measured the effect of rapid monocular stimulation on binocular rivalry dynamics. A subset of participants from Experiment 2 completed a third experiment to determine whether adaptation could explain the results of Experiment 2.

2.1 | Experiment 1: Stimulation parameters for binocular rivalry

2.1.1 | Participants

Nine adults (age range: 21–28 years; five females) with self-reported normal binocular vision participated in a 1-hr binocular rivalry experiment. All participants were informed of the nature of the study before participation and provided written informed consent. The project was approved by the University of Waterloo Research Ethics Committee (ORE #30537; May 2016).

2.1.2 | Stimuli and protocol

Orthogonally oriented sinusoidally modulated gratings were presented dichoptically (57 cm viewing distance) within a circular field subtending 6.1 degrees of visual angle on a gamma-corrected 24-inch Asus® 3D monitor. Relatively large gratings were used because this study was the first step in a program of research that will extend to participants with reduced vision caused by amblyopia. Participants with amblyopia may struggle to see small stimuli. Dichoptic presentation was achieved using red/green anaglyph glasses. The space average contrast levels of the gratings were matched (0.5) using a Chroma Meter CS-100® photometer with measurements made through the anaglyphic filters (mean luminance: red = 8.4 cd/m^2; green = 32.9 cd/m^2). Using a computer keyboard, participants continuously reported whether they perceived the grating presented to the left eye (left eye dominant), the grating presented to the right eye (right eye dominant), or a piecemeal/mixed percept of both gratings. Specifically, a keyboard key was allocated to each percept. Participants held down the key corresponding to their current percept and switched keys when their percept changed. The total duration of each percept as well as the number of alternations (a change from one percept to another) were analyzed.

Participants completed 40 × 60 s randomly sequenced trials—5 trials for each combination of two grating orientation pairs (90/180 versus 45/135 degrees) and four spatial frequencies (0.5, 1, 1.5 or 2 cycles per degree); the spatial frequency of the gratings presented to each eye within a trial was always identical.

2.1.3 | Analysis

Binocular rivalry alternation rates were calculated for each trial separately by dividing the number of alternations (defined as any change in percept) by the total presentation time. Alternation rate calculations included piecemeal percepts. Alternation rates across all five trials were then averaged for each set of stimulus parameters. The cumulative duration of piecemeal percepts was also analyzed. Ocular dominance indices were calculated for each participant as: (time spent viewing with right eye minus time spent viewing with left eye) divided by (total time spent viewing right eye and left eye percepts) to investigate the effect of spatial frequency and orientation on ocular dominance.

Data were tested for normality using the Shapiro-Wilk paired-samples assumption test. Normally distributed data were analyzed using repeated measures ANOVA and post hoc paired *t* tests. Skewed data were analyzed using the Freidman test and post hoc Wilcoxon signed-rank test. We anticipated skewed data across all experiments because the distributions were bounded. Repeated measures ANOVAs or Freidman tests with factors of orientation (90/180 versus 45/135) and spatial frequency (0.5 versus 1.0 versus 1.5 versus 2.0 cpd) were conducted separately for alternation rate, piecemeal duration, and the absolute ocular dominance index. To determine whether stimulus orientation or spatial frequency affected the stability of binocular rivalry dynamics across trials, each participant's standard deviation across trials for each combination of orientation and spatial frequency was calculated for alternation rate. Repeated measures ANOVAs with factors of orientation and spatial frequency were conducted on the standard deviation data. Following the convention in the field, a *p*-value of less than 0.05 was considered statistically significant.

2.2 | Experiment 2: Binocular rivalry following rapid monocular stimulation

2.2.1 | Participants

Twenty-five adults (mean age 25, range 19–33; 21 female) with normal binocular vision based on stereopsis of ≤40 arc sec (The Fly Stereo Acuity Test®, Vision Assessment Corporation) and normal or corrected-to-normal vision (0.1 logMAR or better in each eye) participated in the rapid monocular stimulation experiment. Exclusion criteria included any neurological condition or the use of psychoactive drugs. All participants were informed of the nature of the study before participation and provided written informed consent. The project was approved by the University of Waterloo Research Ethics Committee (ORE #30537; May 2016).

2.2.2 | Rivalry stimulus

The stimulus spatial frequency and orientation pair determined in Experiment 1 (0.5cpd, 45/135 degrees) was chosen for this experiment. Viewing conditions and the method of reporting binocular rivalry percepts were

identical to Experiment 1. Three 60-s trials of binocular rivalry were recorded before and after rapid monocular stimulation.

2.2.3 | Study design

We used a modified version of the rapid monocular stimulation protocol described by Teyler et al. (2005) (Figure 1). Within a repeated measures design, participants completed two study conditions on separate days: a rapid monocular visual stimulation condition and a binocular control condition. Upon the first visit, participants completed either the rapid monocular stimulation condition or the binocular control condition, assigned randomly. Rapid monocular stimulation involved monocular viewing of only one of the two gratings that made up the binocular rivalry stimulus flickering on and off (50% duty cycle, on: high contrast grating on a luminance-matched grey surround; off: uniform grey field) at 9 Hz for 2 min. The stimulated eye was randomly selected for each participant. The stimulated eye was stimulated with the same grating orientation that was presented to that eye during the pre and poststimulation binocular rivalry measures because the LTP-like effects of rapid visual stimulation are stimulus-specific. Participants wore red/green glasses during the rapid monocular stimulation. The binocular control condition was identical except that the two gratings that made up the binocular rivalry stimulus were alternated in the center of the monitor at 9 Hz and viewed binocularly (no red/green glasses). In both the rapid monocular stimulation and binocular control conditions, the 2 min of visual stimulation was followed by 2 min of eye closure to minimize adaptation effects. Binocular rivalry measures were recorded before stimulation (pre) and after eyelid closure (post).

2.2.4 | Analysis

The binocular rivalry measures were alternation rate, time spent in piecemeal, and ocular dominance index (all calculated as in Experiment 1). Alternation rates and time spent in piecemeal across all three trials were averaged for each condition. An ocular dominance index was calculated for each participant based only on the duration of left eye dominant and right eye dominant percepts. Piecemeal percepts were not included in this analysis. In the rapid monocular stimulation condition this index was defined as: (stimulated eye dominance duration minus non-stimulated eye dominance duration) divided by the sum of dominance durations for the two eyes; in the binocular control condition, the ratio was calculated in the same way based on the eye randomly selected for stimulation in the monocular condition.

Data were analyzed using parametric or non-parametric tests depending on normality as in Experiment 1. ANOVAs or Freidman tests with factors of Condition (rapid monocular stimulation versus control) and Time (pre versus poststimulation) were conducted separately for alternation rate, piecemeal duration, and ocular dominance indices. Post hoc testing was conducted using paired *t* tests or the Wilcoxon signed-rank test.

2.3 | Experiment 3: Binocular rivalry following monocular adaptation

2.3.1 | Participants and methods

A subset of participants that completed Experiment 2 who consented to and were available for additional testing ($N = 12$) completed Experiment 3 on a separate day several months after completing Experiment 2. Experiment 3 was a post hoc experiment designed to investigate whether monocular adaptation

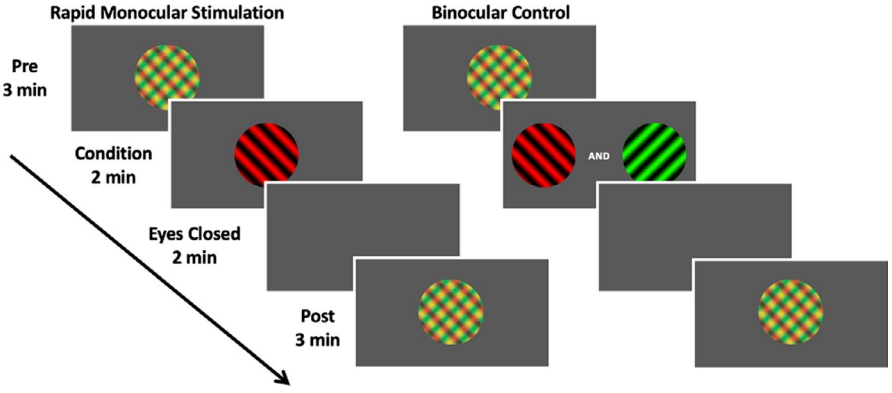

FIGURE 1 Schematic representation of Experiment 2 protocol. Plaid stimuli indicate binocular rivalry testing. In the rapid monocular stimulation condition, one of the gratings that made up the plaid was presented monocularly and flickered at 9 Hz. The stimulated eye (and therefore the red or green colour of the grating) was randomised. In this figure, the red grating is shown as an example. In the control binocular condition, the two gratings that made up the binocular rivalry stimulus were alternated at 9 Hz at the center of the screen and were viewed binocularly

could explain the results of Experiment 2. The pre and post measurements of binocular rivalry used in Experiment 3 were identical to those used in Experiment 2. The monocular adaptation between the pre and post tests was a static monocular presentation of one of the gratings that made up the binocular rivalry stimulus for 2 min. The static grating was presented to the same eye (left or right) that had been exposed to rapid monocular stimulation in Experiment 2. As in Experiment 2, participants closed their eyes for 2 min following adaptation.

2.3.2 | Analysis

Two analyses were conducted. First, the results from the rapid monocular stimulation and control conditions in Experiment 2 were reanalyzed using only data from the subset of participants who completed Experiment 3 to test whether the main finding from Experiment 2 (reduced ocular dominance index for the stimulated eye in the rapid monocular stimulation condition but not the control condition) was present in the smaller sample. Wilcoxon signed-rank tests were used to compare the ocular dominance indices pre versus poststimulation in the rapid monocular stimulation and control conditions. Second, a Wilcoxon signed-rank test was conducted on the data collected in Experiment 3 to compare ocular dominance indices pre versus post static visual adaptation of one eye.

3 | RESULTS

3.1 | Experiment 1

For alternation rates, a repeated measures ANOVA showed no significant effects of Grating Orientation ($p > 0.05$; Figure 2a). However, a main effect of Grating Spatial Frequency was observed ($F_{1,8} = 4.194$, $p = 0.016$, $r^2 = 0.028$; Figure 2b, Table 1). Alternation rates were slowest at 0.5 cpd. Alternation rates for the 0.5 cpd stimulus differed significantly from the 1 cpd ($t_8 = -3.617$, $p = 0.007$, Cohen's $d = -1.206$) and 1.5 cpd ($t_8 = -3.485$, $p = 0.008$, Cohen's $d = -1.162$) stimuli, but not the 2 cpd stimulus ($t_8 = -1.597$, $p = 0.149$, Cohen's $d = -0.532$). No significant effects of Grating Orientation or Grating Spatial Frequency were observed for piecemeal duration or for the standard deviations of alternation rate (all $F < 3.903$, all $p > 0.069$). Absolute values of ocular dominance indices were not normally distributed. As a result, the Freidman test was conducted and showed no significant effect of Grating Orientation ($F_1 = 0.130$, $p = 0.716$, Kendall's W = −567.8) or Grating Spatial Frequency ($F_1 = 2.641$, $p = 0.062$, Kendall's W = −21.9) on ocular dominance index. Based on these results, a spatial frequency of 0.5 cpd was chosen for Experiment 2 because this spatial frequency induced the slowest alternation rates. The oblique orientations (45/135) were chosen for Experiment 2 arbitrarily.

TABLE 1 Effects of grating spatial frequency on binocular rivalry

Spatial frequency	Alternation rate[a] (Hz)	Piecemeal[a] (time/60 s)	Absolute ocular dominance index[a]
0.5 cpd	0.49 (±0.18)	0.06 (±0.02)	0.11 (±0.07)
1.0 cpd	0.57 (±0.19)	0.10 (±0.03)	0.11 (±0.04)
1.5 cpd	0.56 (±0.18)	0.12 (±0.04)	0.16 (±0.10)
2.0 cpd	0.54 (±0.16)	0.13 (±0.04)	0.20 (±0.16)

[a]Grand mean between subjects followed by the mean of the within subject standard deviations.

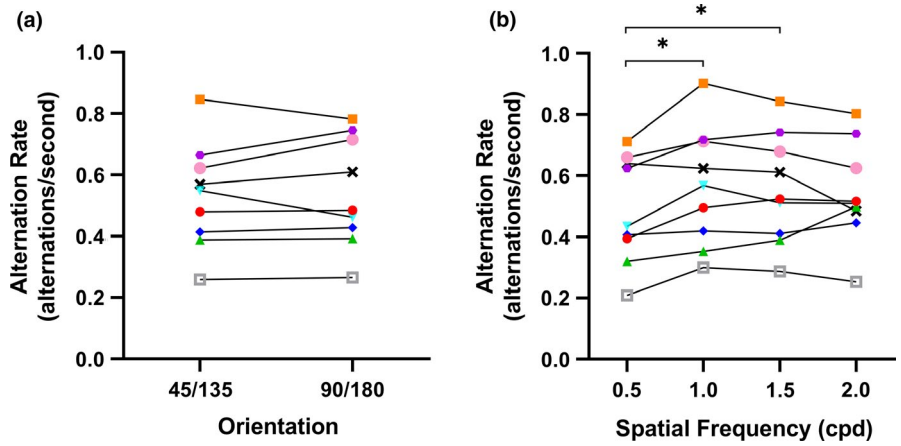

FIGURE 2 Rivalry alternation rates for Experiment 1. (a) Orientation with mean alternation rates for each individual participant collapsed across spatial frequency. (b) Spatial frequency with mean alternation rates for each individual participant collapsed across orientation. Each color signifies a different participant ($n = 9$). (*) indicates significant differences for group post hoc paired t tests $p < 0.05$

3.2 | Experiment 2

Neither alternation rates nor ocular dominance indices were normally distributed. Therefore, nonparametric statistics were adopted. The median values ± interquartile ranges for measures of rivalry dynamics pre and post rapid monocular stimulation were 0.60 ± 0.24 Hz and 0.56 ± 0.24 Hz for alternation rates (Figure 3), 8.46 ± 10.13 s and 11.96 ± 12.33 s for time spent in piecemeal (Figure 4), and 0.02 ± 0.12 and −0.05 ± 0.08 for ocular dominance indices (Figure 5). For the binocular control condition, medians pre and post stimulation were 0.65 ± 0.28 and 0.61 ± 0.27 for alternation rates, 12.51 ± 11.71 s and 13.71 ± 13.95 s for time spent in piecemeal, and −0.01 ± 0.09 and −0.02 ± 0.16 for ocular dominance indices. Rapid monocular stimulation did not alter binocular rivalry alternation rates (Freidman test: no effect of Condition [rapid monocular stimulation versus binocular control]; $F_1 = 3.137$, $p = 0.081$, Kendall's W = −17.9), or the duration of piecemeal percepts (Freidman test: no effect of Condition [rapid monocular stimulation versus binocular control]; $F_1 = 3.229$, $p = 0.077$, Kendall's W = −18.1). However, rapid monocular stimulation shifted the ocular dominance index in favor of the non-stimulated eye (Freidman test: significant effect of Condition [rapid monocular stimulation versus binocular control]; $F_1 = 5.332$, $p = 0.025$, Kendall's W = −18.8). The effect was associated with a significant shift in ocular dominance index toward the non-stimulated percept for the rapid monocular stimulation condition (post hoc Wilcoxon signed-rank test, W = 248.0, $p = 0.005$, $r = 0.653$; Figure 5). In other words, rapid monocular stimulation decreased the time spent viewing the percept for the stimulated eye relative to that for the non-stimulated eye. There was no change in ocular dominance index for the binocular control condition (W = 134.5, $p = 0.668$, $r = -0.103$).

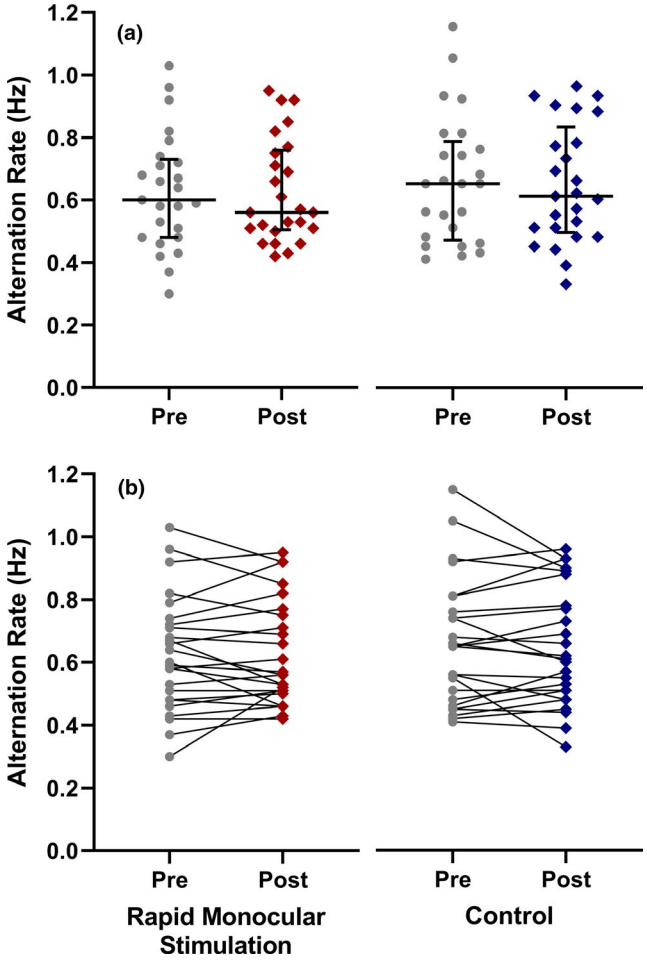

FIGURE 3 Individual alternation rates for the rapid monocular stimulation and binocular control conditions in Experiment 2 presented as scatter (a) and line (b) plots. Solid horizontal lines in panel a denote medians; error bars = IQR

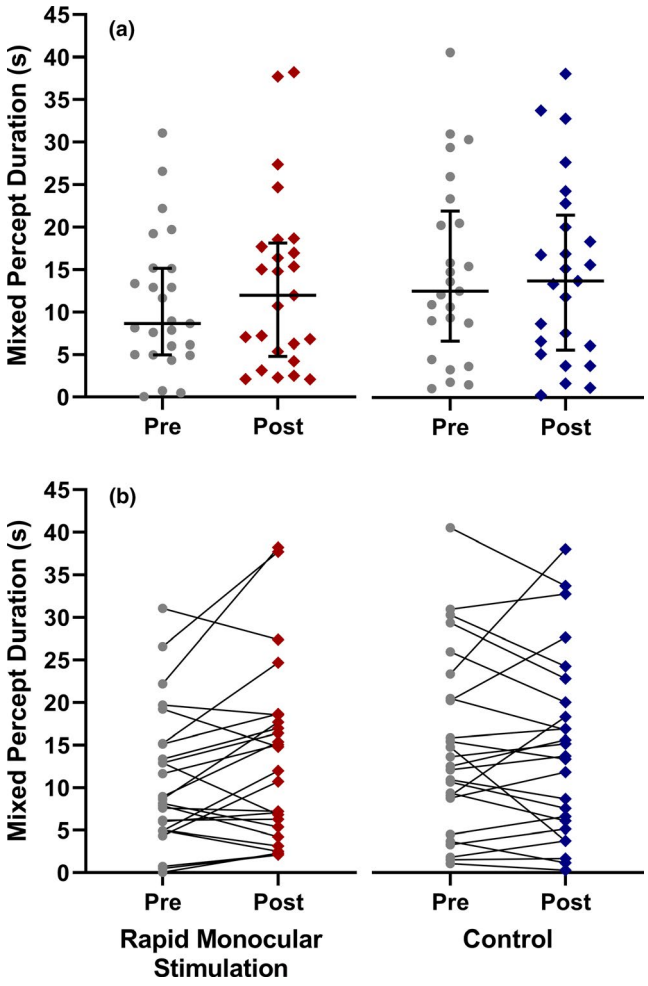

FIGURE 4 Time in piecemeal for the rapid monocular stimulation and binocular control conditions from Experiment 2 presented as scatter (a) and line (b) plots as in Figure 3

3.3 | Experiment 3

Experiment 3 data were not normally distributed. For the subgroup from Experiment 2 who also completed

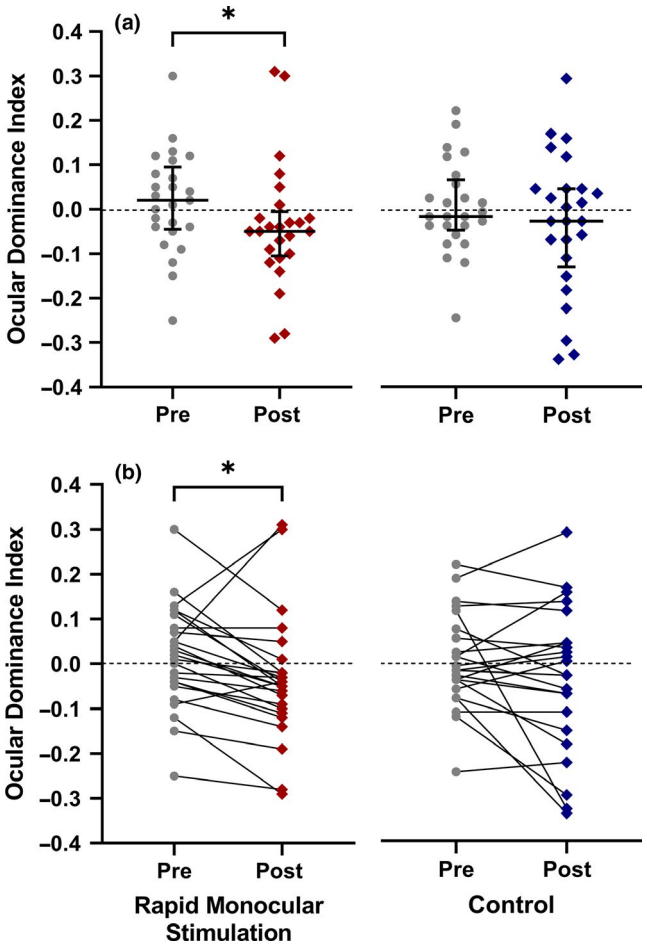

FIGURE 5 Median ocular dominance indices for the rapid visual stimulation and binocular control conditions in Experiment 2 presented as scatter (a) and line (b) plots as in Figure 3. Negative values indicate decreased dominance for the stimulated eye

Experiment 3, monocular adaptation did not alter ocular dominance (W = 30.0, $p = 0.838$, $r = 0.091$). Importantly, this subgroup did show a significant shift in ocular dominance toward the non-stimulated eye following rapid monocular stimulation, similar to that of the full cohort in Experiment 2 (W = 66.0, $p = 0.004$, $r = 1.000$; Figure 6). This subgroup also showed no effect of the binocular control condition from their Experiment 2 data (W = 32.0, $p = 0.610$, $r = -0.179$).

4 | DISCUSSION

The primary aim of this study was to assess whether rapid monocular stimulation of one eye would increase the dominance of that eye during binocular rivalry. Unexpectedly, we observed the opposite effect; rapid monocular stimulation *reduced* the relative dominance of the stimulated eye during binocular rivalry.

How might we explain this unexpected result? The simplest explanation is that rapid monocular stimulation caused retinal or cortical adaptation resulting in reduced dominance of the stimulated eye during binocular rivalry. Following previous work (Teyler et al., 2005), our rapid monocular stimulation protocol was designed to minimize adaptation effects by providing a period of eye closure directly after the rapid visual stimulation that was the same duration as the rapid visual stimulation itself (2 min). Generally, a period of adaptation lasts as long as the stimulation (Greenlee et al., 1991; see Başgöze et al., 2018 for an in-depth review). However, it is still possible that adaptation played a role in our results. Therefore, we conducted a third experiment on a subset of participants from Experiment 2 who were available and willing to complete further testing. This experiment revealed that simply adapting one eye to one of the gratings that made up the binocular rivalry stimulus did not alter ocular dominance. Although the sample size for this experiment was smaller than for the main experiment and therefore had less power to detect small shifts in ocular dominance, there was no trend observed to indicate adaptation. Together, the use of a period of eye closure within our rapid monocular stimulation protocol and the results of Experiment 3 argue against adaptation as an explanation of our unexpected result.

An alternative explanation is that the rapid visual stimulation of one eye may not have generated the expected LTP-like effects but rather a long-term depression-like effect (LTD). Although increased cortical excitability is the most commonly reported effect of visual stimulation (Clapp, et al., 2006; de Gobbi Porto et al., 2015; Kirk et al., 2010; Teyler et al., 2005), decreased or inconsistent changes in cortical activity have also been reported. These include a reduced visual cortex BOLD response post-stimulation (Lahr et al., 2014) and reduced VEP amplitude in young adults post stimulation (Abuleil et al., 2019). The reason that some studies show LTP-like and others show LTD-like results is not clear; however, this pattern of results does suggest that visual stimulation effects are inconsistent (Sanders et al., 2018). LTD-like changes following visual stimulation would be consistent with our observation of relatively reduced binocular rivalry dominance for the eye that received rapid monocular stimulation.

One additional possible explanation for decreased dominance following rapid monocular stimulation is suggested by recent studies that have explored the effect of short-term monocular occlusion on binocular rivalry dominance. After one eye is occluded for a period of time, that eye has a relative increase in dominance during binocular rivalry once the occlusion is removed (Lunghi et al., 2011; Min et al., 2018). Furthermore, this effect does not require full occlusion of the deprived eye. For example, induced suppression of one eye or the presentation of lower contrast images to one eye for as little as 3 min also increases that eye's binocular rivalry

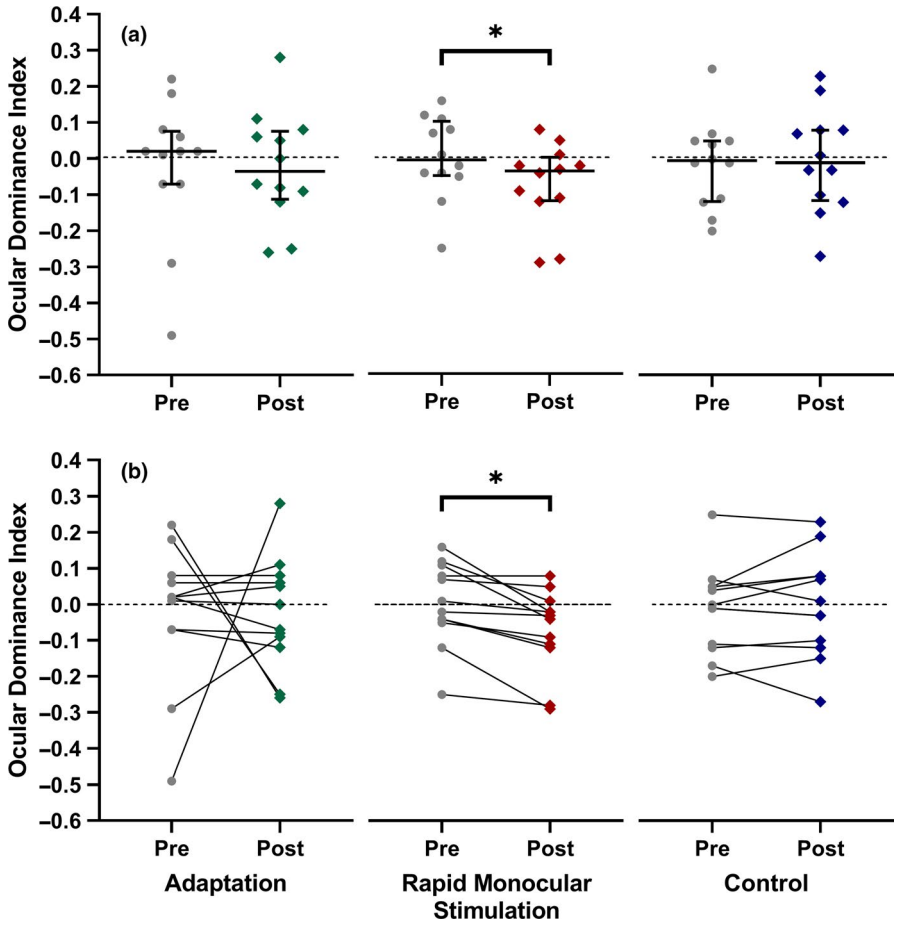

FIGURE 6 Ocular dominance indices for participants who completed both Experiment 2 and Experiment 3 ($n = 12$) presented as scatter (a) and line (b) plots as in Figure 3. Negative values indicate reduced dominance for the stimulated/adapted eye

dominance (Kim et al., 2017). Other image degradation manipulations such as the presentation of pink noise (Bai et al., 2017) or spatial scrambling of one eye's image also result in increased dominance of the deprived eye over the eye exposed to normal visual stimulation (Ramamurthy & Blaser, 2018; Zhou et al., 2014). The effects of short-term monocular occlusion also extend to participants with amblyopia, a disorder characterized by chronic perceptual dominance of the fellow eye over the amblyopic eye (Li et al., 2011). Occlusion of the amblyopic eye strengthens the contribution of that eye to binocular vision once the occlusion is removed (Chadnova et al., 2017; Lunghi et al., 2011, 2016, 2019; Zhou et al., 2013, 2019).

Possible mechanisms underlying the ocular dominance shift induced by short-term monocular occlusion include a change in neural interocular gain control resulting from a large imbalance in the input from each eye to cortical processing (Lunghi et al., 2011; Zhou et al., 2013). This change is associated with reduced visual cortex GABA concentration (Lunghi et al., 2015) and may involve both feedforward and feedback pathways (Ramamurthy & Blaser, 2018).

The effect of monocular deprivation on binocular rivalry typically requires a longer period of deprivation than 2 min (Lunghi et al., 2015). However, it is possible that LTP-like changes in the visual cortex induced by monocular rapid visual stimulation drive a more abrupt plastic change. In particular, we postulate that the strengthening of the cortical response to the stimulated eye generated by our monocular rapid stimulation protocol rapidly activated the same homeostatic mechanisms that underpin short-term monocular occlusion effects. In other words, the reduced binocular rivalry dominance of the stimulated eye was not a direct effect of the rapid monocular stimulation but was caused by the relative deprivation of the non-stimulated eye.

Our study had a number of limitations. As mentioned above, the sample size for Experiment 3 was limited. Additional experiments with a larger sample size will be required to fully explore the effect of monocular adaptation on binocular rivalry for our stimuli. In addition, while the focus of our study was the effect of rapid monocular visual stimulation on binocular rivalry dynamics, further investigation is needed to identify the optimal visual stimulus parameters for the induction of LTP-like or LTD-like effects. Temporal frequency is likely to be a particularly important parameter. Electroencephalography (EEG) recordings may also provide further insight into the neural mechanisms driving the effect of rapid monocular visual stimulation on binocular rivalry. Additionally, we did not measure the optimal duration of monocular rapid visual stimulation for altering eye dominance in binocular rivalry or the length of time for which

eye dominance was altered. It has previously been observed that 2 min of rapid visual stimulation increased VEP amplitudes, while 10 min of stimulation had no effect (Normann et al., 2007). In addition, the effect of rapid visual stimulation on VEP/ERP amplitude has been reported to last for up to an hour or until the effect is measured using a slow 1 Hz stimulus (Clapp et al., 2006; Teyler et al., 2005). It is currently unknown whether these results also apply to the behavioral effects of rapid visual stimulation.

As a whole, our results raise the exciting possibility that rapid monocular stimulation can be used to rapidly induce eye dominance shifts. Potential applications of this technique include the manipulation of ocular dominance in amblyopia. We are currently conducting studies that address this possibility.

ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council (NSERC) grants RPIN-05394 and RGPAS-477166 as well as the Canadian Foundation for Innovation (CFI) grant 34095. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Abuleil, McCulloch, and Thompson contributed equally to the research design, data collection, and writing of the study. Patterson contributed only to data collection.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ejn.14971

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on Figshare: Abuleil, Dania; McCulloch, Daphne; Patterson, Heidi; Thompson, Benjamin (2020): LTP_BinocularRivalryModulation.xlsx. figshare. Dataset. https://doi.org/10.6084/m9.figshare.12867341.v1

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How to cite this article: Abuleil D, McCulloch DL, Patterson H, Thompson B. Modulation of binocular rivalry with rapid monocular visual stimulation. *Eur. J. Neurosci.*2020;00:1–11. https://doi.org/10.1111/ejn.14971