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Binocular vision adaptively suppresses delayed monocular signals

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Abstract

A neutral density filter placed before one eye will produce a dichoptic imbalance in luminance, which attenuates responses to visual stimuli and lags neural signals from retina to cortex in the filtered eye. When stimuli are presented to both the filtered and unfiltered eye (i.e., binocularly), neural responses show little attenuation and no lag compared with their baseline counterpart. This suggests that binocular visual mechanisms must suppress the attenuated and delayed input from the filtered eye; however, the mechanisms involved remain unclear. Here, we used a Steady-State Visual Evoked Potential (SSVEP) technique to measure neural responses to monocularly and binocularly presented stimuli while observers wore an ND filter in front of their dominant eye. These data were well-described by a binocular summation model, which received the sinusoidal contrast modulation of the stimulus as input. We incorporated the influence of the ND filter with an impulse response function, which adjusted the input magnitude and phase in a biophysically plausible manner. The model captured the increase in attenuation and lag of neural signals for stimuli presented to the filtered eye as a function of filter strength, while also generating the filter phase-invariant responses from binocular presentation for EEG and psychophysical data. These results clarify how binocular visual mechanisms—specifically interocular suppression—can suppress the delayed and attenuated signals from the filtered eye and maintain normal neural signals under imbalanced luminance conditions.

Keywords: Neutral Density filter, Steady-State Visual Evoked Potential, Binocular Summation, Binocular Interactions, Binocular Rivalry, Binocular Vision, Luminance, Gain Control, Suppression

1 Introduction

Neural and perceptual responses to visual stimuli are modulated by the mean luminance of the visual field: under low luminance levels, visual responses are impoverished and sensitivity to spatial and temporal contrast patterns is poor (De Valois et al., 1974; Kilpeläinen et al., 2012, 2011; Shapley and Enroth-cugell, 1984; Swanson et al., 1987). If luminance is lowered in only one eye (i.e., a dichoptic luminance change), the reduced stimulus intensity to the darkened eye will—in turn—alter binocular function, and hinder performance on a series of binocular measures including binocular summation, binocular rivalry, and stereo acuity (Baker, Meese, & Hess, 2008; Baker, Meese, Mansouri, & Hess, 2007; Chang et al., 2006; De Valois et al., 1974; Gilchrist & Pardhan, 1987; Leonards & Sireteanu, 1993; Zhou, Jia, Huang, & Hess, 2013). For example, binocular summation can be abolished and return to monocular performance levels when transmittance is reduced to 3% (Baker et al., 2007b), while the proportion and duration of dominance events of the darkened eye in binocular rivalry decrease in proportion to the decrement in luminance (Leonards and Sireteanu, 1993). This is thought to occur because the reduced responses of the darkened eye push the binocular functional balance towards that of the unaffected eye. That is, interocular interactions adaptively suppress signals from the filtered eye and minimize its contribution to the binocular percept. This process is similar to that thought to underlie visual deficits observed in individuals with binocular vision disorders (e.g., amblyopia), and investigating the architecture of this functional balance may help elucidate the functional visual imbalances experienced by these individuals (Baker, Meese, Mansouri, et al., 2007; Campbell, Maffei, & Piccolino, 1973; De Belsunce & Sireteanu, 1991; Heravian-Shandiz, Douthwaite, & Jenkins, 1991; Leonards & Sireteanu, 1993; Zhang, Bobier, Thompson, & Hess, 2011).

An interocular imbalance in luminance limits binocular interactions as it reduces the response magnitude and slows the response latency of cells selective for the darkened eye, which generates an asynchrony between the signals from each eye (Heravian-Shandiz et al., 1991; Katsumi, Tanino, & Hirose, 1986; Spafford & Cotnam, 1989; Wilson & Anstis, 1969). While both the attenuation and slowing of responses can be estimated psychophysically (Harker and O'Neal, 1967; Lit, 1949; Morgan and Thompson, 1975), they can also be directly measured in human observers with EEG methods, by recording either transient (VEPs) or steady-state Visual Evoked Potentials (SSVEPs) to stimuli presented under different luminance levels (Heravian-Shandiz et al., 1991; Katsumi et al., 1986; Norcia et al., 2015; Spafford and Cotnam, 1989). Response lags under low transmittance conditions (1% or a 2.0ND filter) can reach values up to 80ms and a 50% decrease in response magnitude in the darkened eye (Chadnova et al., 2018; Heravian-Shandiz et al., 1991; Spafford & Cotnam, 1989). This impairment is generally absent when stimuli are presented to both the darkened and un-filtered eye (i.e., binocularly): transient and SSVEPs show little difference from normal viewing conditions, which indicates that some type of compensatory neural mechanism can suppress the delayed and attenuated neural signals from the darkened eye (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). A comprehensive description of the visual mechanism able to maintain normal signal transmission under binocular viewing when interocular responses are asynchronous remains to be defined.

There are cues from previous studies that point towards a model architecture able to predict the effects of an interocular luminance imbalance. For example, Chadnova et al. (2018*)* found that a binocular contrast normalization model, which received as input the temporal signals (stimulus oscillation) filtered by an impulse response function, was able to describe the attenuation and delay of SSVERs (Steady-State Evoked Responses, recorded with MEG) generated by a 1.5ND filter (3% transmittance) placed before one eye. However, they frequency tagged their stimuli so that each eye (the darkened and un-filtered eye) was presented with stimuli that oscillated at different frequencies (4Hz and 6Hz). While this allowed them to measure independent responses from both eyes under dichoptic viewing, it prevented them from measuring responses to a fused binocular stimulus, so they could not measure or model normal signal transmission to binocularly presented stimuli when luminance levels differ between the eyes.

Modern models of binocular vision describe binocular combination as a two-stage process of contrast gain control, in which normalized monocular signals are linearly summed prior to undergoing a second normalization stage. Crucially, the monocular terms in these models include interocular interactions, which modulate the signals from each eye by that of the other eye (Baker et al., 2008; Ding and Sperling, 2006; Huang et al., 2010; Meese et al., 2006; Zhou et al., 2013). This model architecture can account for a wide range of psychophysical phenomena, including dichoptic masking, binocular summation at threshold, the converging of monocular and binocular discrimination thresholds at suprathreshold contrast levels, and the combination of dichoptically presented phase incongruent stimuli (Baker et al., 2008, 2007c; Ding and Sperling, 2006; Georgeson et al., 2016; Heeger, 1992; Legge, 1984a, 1984b; Meese et al., 2006). It follows that this type of model would be ideally suited to describe the mechanism responsible for maintaining normal signal transmission when luminance levels differ between the eyes. Indeed, this has been demonstrated psychophysically by using a modified version of the Ding and Sperling (2006) binocular combination model to define the perceptual effects of an imbalance of luminance between both eyes on a phase combination task (Zhou et al., 2013). Their model predicted the gradual transition in perceived phase towards that of the un-filtered eye as the transmittance of the filter in the darkened eye was reduced (i.e., increasing the density). However, given the nature of their paradigm, only the reduction in response amplitude from the filtered eye could be accounted for—they could not empirically test the ability of their model to explain temporal asynchronies generated by low luminance in the darkened eye.

Here, we recorded SSVEPs to monocularly and binocularly presented flickering sinusoidal gratings while observers wore ND filters of various transmittances before their dominant eye. To verify that the attenuation and lag recorded from our SSVEPs are representative of the observers' percept, we measured binocular summation and binocular rivalry under the same ND filter conditions as the SSVEP portion of our study. Finally, we implement the two-stage contrast gain control model proposed by Meese et al., (2006) in an effort to define the mechanism that suppresses the attenuated and delayed monocular signals from the darkened eye in order to maintain normal signal transmission under binocular viewing. We adapt the psychophysical two-stage contrast gain control model to generate neural response amplitude and latency values under various monocular reductions in luminance by convolving the input to the model with an Impulse Response Function experimentally derived for the transmittance of a given ND filter (Swanson et al., 1987), similar to previous approaches of modelling SSVEP amplitude and phase (Chadnova, et al., 2018; Cunningham et al., 2017). As expected, SSVEP amplitude decreased and latency increased as a function of ND filter transmittance for monocularly viewed stimuli, while little change was observed under binocular viewing, consistent with previous reports (Heravian-Shandiz et al., 1991; Katsumi et al., 1986; Spafford and Cotnam, 1989). These effects were well explained by our model, which generated response amplitude and response latencies that that mirrored that of our observers both in the monocular and binocular viewing conditions. Additionally, our model captured the effects of a decrease in luminance on binocular summation without any additional parameter adjustments. Taken together, our neurophysiological findings, psychophysical findings, and modelling demonstrate that standard interocular interactions in binocular vision paired with response attenuation is sufficient to maintain normal signal transmission from discordant and asynchronous monocular signals.

2 Methods

2.1 Participants

Nine observers (2 males: authors BR and DHB), with normal or corrected to normal visual acuity participated in this study (M_{age} = 25 years, SD = 4.24). Written informed consent was obtained from all participants, and experimental procedures were approved by the ethics committee of the Department of Psychology at the University of York.

2.2 Apparatus

All stimuli were presented using a gamma corrected ViewPixx 3D display (VPixx technologies, Canada) driven by a Mac Pro. Binocular separation with minimal crosstalk was achieved by synchronizing the refresh rate of the display with the toggling of a pair of Nvidia stereo shutter goggles using an infra-red signal. Monitor refresh rate was set to 120Hz, meaning that each eye was updated at 60Hz (every 16.67 msec). Display resolution was set to 1920 X 1080 pixels. A single pixel subtended 0.027° of visual angle (1.63 arc min) when viewed from 57 cm. The mean luminance of the display viewed through the shutter goggles was 26 cd/m^2.

EEG signals were recorded from 64 electrodes distributed across the scalp according to the 10/20 EEG system (Chatrian et al., 1985) in a WaveGuard cap (ANT Neuro, Netherlands). We monitored eye blinks with an electrooculogram, which consisted of bipolar electrodes placed above the eyebrow and atop of the cheek on the left side of the participant's face. Stimulus-contingent triggers were sent from the ViewPixx display to the amplifier using a parallel cable. Signals were amplified and digitized using a PC with the ASAlab software (ANT Neuro, Netherlands). All EEG data were imported into MATLAB (Mathworks, MA, USA) and analysed offline.

2.3 Stimulus

Stimuli were four 3 cycles/° horizontal sinusoidal gratings, windowed by a raised cosine envelope to subtend 5° of visual angle on the retina. The stimuli were tiled to have a grating above, below, to the right, and to the left of fixation (see **Figure 1**). Distance between the centre of the gratings and fixation was set to 5°. To promote binocular fusion, two oblique lines crossing at the centre of the display were shown to both eyes throughout the experiment. To measure contrast response functions, stimulus contrast—expressed in decibels ($C_{dB} = 20\log_{10}(C_{\%})$)—ranged between 15.6dB and 39.6dB (6% to 96% Michelson Contrast) in steps of 6dB. Stimulus contrast was fixed at 39.6dB for SSVEPs measured with ND filters. The stimulus flicker (on/off contrast modulation) was set to 5Hz and followed a sinusoidal waveform in negative cosine phase rescaled to the range from 0-1: stimulus contrast began at 0%, increased smoothly to 100% of the nominal maximum, and then returned to 0% over a period of 200ms (i.e., 1 cycle).

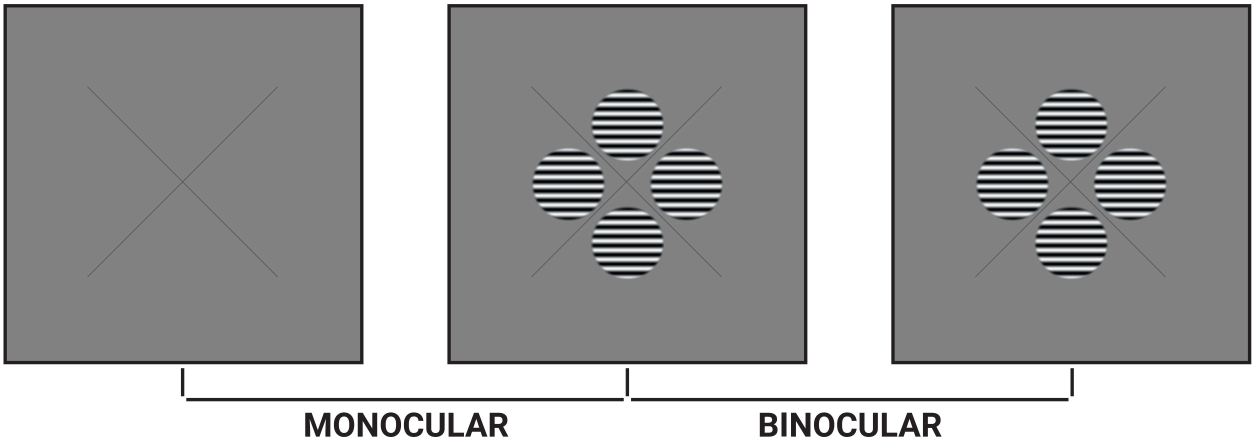

Figure 1. Example stimulus display for monocular and binocular viewing conditions. Under monocular viewing, only a single eye was presented with the flickering stimuli while the other eye saw a screen set to mean luminance with the fusion cross. Under binocular viewing conditions, both eyes were presented with identical stimuli flickering in phase at a rate of 5Hz. The spatial frequency of these gratings has been adjusted for print quality.

2.4 Procedures

SSVEP contrast response functions were measured monocularly (dominant and non-dominant eye) and binocularly. Stimuli flickered on screen for 11 seconds and were followed by a screen set to mean luminance—with the fusion cross—for 3 seconds. In monocular trials, the un-stimulated eye was presented with a screen set to mean luminance with a fusion cross. In binocular trials, observers were presented with identical displays to each eye that flickered in-phase—note that as we used shutter goggles to present stimuli to observers, there is a slight offset between the contrast of the stimuli presented to the left and right eye as they are sampled from slightly different points along the sinusoidal modulation. Observers completed 8 trials per stimulus contrast (15.6, 21.6, 27.6, 33.6, 39.6 dB) and viewing condition, for a total of 120 trials (~30 minutes of viewing time). Participants were given the opportunity to rest every 30 trials.

To measure the effects of an interocular imbalance in luminance on the amplitude and latency of neural signals, we fitted participants with an ND filter over their dominant eye (measured with the Miles Test; Miles, 1930). Participants viewed the same sinusoidal gratings as those defined above (only at maximum contrast: 39.6 dB) either in the filtered eye alone (monocularly) or binocularly. Presentation duration and the inter-trial intervals were identical to those of the contrast response function measurements. Three neutral density filters, with strength 0.6ND (25 % transmittance), 1.2ND (6% transmittance) and 1.8ND (1.6% transmittance) were used to reduce the luminance in the filtered eye. Observers completed 8 trials for each ND filter strength and viewing condition (monocular and binocular), for a total of 48 trials—approximately 12 minutes of viewing time.

Measurements of the contrast response functions and the ND filter conditions were completed in this order during the same experimental session. Thus, observers were adapted to the mean luminance of the display (26cd/m^2) for approximately 30 minutes prior to completing the ND filter conditions (with some variability in the duration of breaks taken by observers), which ensures minimal variability in their sensitivity to light as dark adaptation curves taper after 30 minutes in the dark (Lamb and Pugh, 2004; Pugh, 1975). Stimulus contrast and ND filter strength were randomized across trials and participants, respectively. Observers were given no explicit task other than to fixate at the centre of the fusion cross and minimize blinking during stimulus presentation.

3 SSVEP Analysis

We used whole-head average referencing to normalize each electrode to the mean signal of all 64 electrodes (for each sample point). Prior to data analysis, the first second of each trial (single trial duration: 11 seconds) was discarded to eliminate onset transients while the remaining 10 seconds were Fourier transformed. Example spectra from a single observer for the contrast response function measurement and the ND filter conditions are shown in **Figure 2A,** the scalp distributions of SSVEP amplitudes at the fundamental frequency (5Hz) for stimuli of increasing contrast in **Figure**

2B, and ND filters of increasing strengths in **Figure 2C**. Across all viewing conditions, the largest and most reliable Fourier component was at the fundamental frequency of our stimulus flicker (5Hz). Steady-state amplitudes at the third harmonic (15Hz) offered no additional information to those of the fundamental while the second harmonic (10Hz) lay in the center of the alpha band (Strasburger, 1987), which made steady-state amplitudes small and quite variable across viewing conditions and participants. We thus concentrated our analyses on the amplitude and phase values of the fundamental frequency and did not include the Fourier amplitude or Fourier phase values from higher harmonics in our analyses. We decided to analyze SSVEPs at four electrodes: Oz, O1, O2, and POz, concentrated at the back of the head (where the largest EEG signals were recorded; see **Figure 2B-C**).

The Fourier amplitude value for the 5Hz component was averaged using conventional methods: we took the coherent average of SSVEP amplitude across the four electrodes, followed by trials (n = 8 repetitions), and then took the incoherent average across observers. As Fourier phase is a circular statistic, the mean angle of phase values for the 5Hz component (ρ) were averaged by taking the sum of complex numbers of unit magnitude $e^{i\theta}, \rho_\theta = \sum_{n=1}^{N} e^{i\theta_n}$, where θ_n is the measured phase angle for a given trial. The circular standard deviation of the average Fourier phase was calculated as $sd_\theta = \sqrt{-2\log\|\rho_\theta\|}$, where $\|\rho_\theta\|$ is the resultant vector length $\left(\frac{|\rho_\theta|}{N}\right)$. Response delays were defined as the difference between the Fourier phase angle recorded for viewing conditions with an ND filter and their no filter counterparts, described by the ratio $\Delta_\theta = \frac{e^{i\theta_{ND}}}{e^{i\theta_0}}$. The angular difference was then averaged across observers in the same manner as defined above, and the resulting value was taken as the average response lag in degrees attributable to the ND filters.

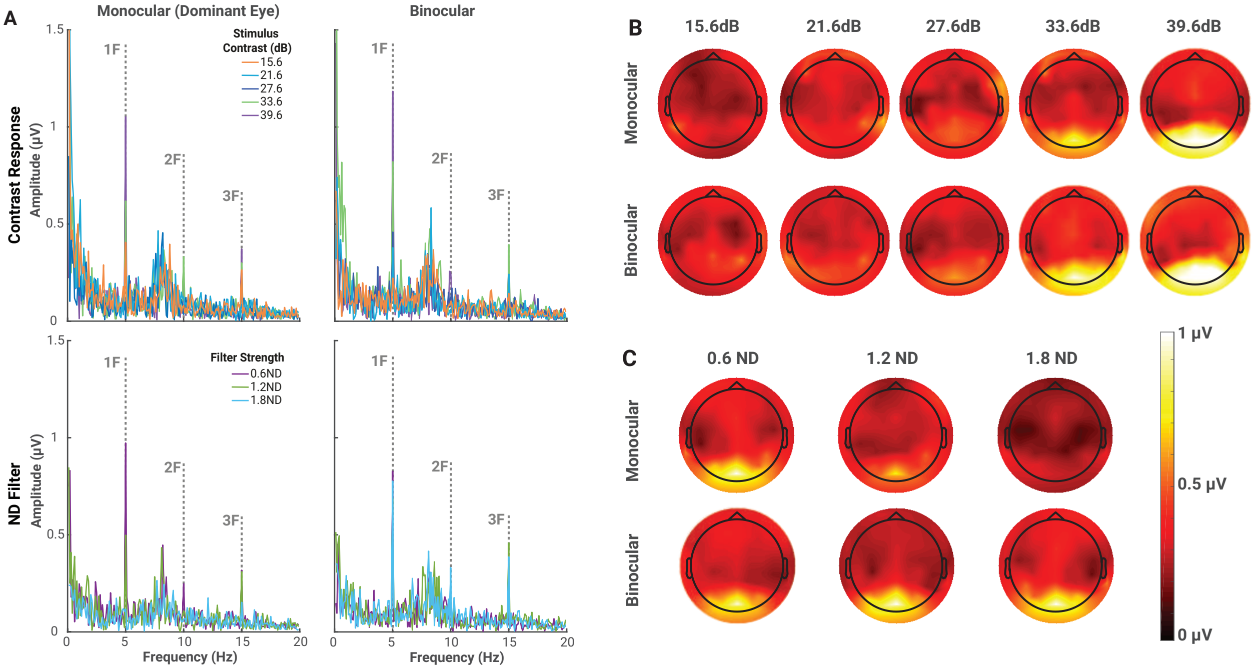

Figure 2. A Example Fourier Spectra for SSVEPs collected from one observer. The top row shows the Fourier amplitude of frequencies up to 20Hz for stimuli of different contrasts, for dominant eye monocular (left panel) and binocular (right panel) presentations. The bottom row shows Fourier amplitudes for the ND filter conditions. Fourier amplitude was greatest at the fundamental frequency of the stimulus flicker (5Hz), whereas the higher harmonic amplitudes (10 & 15Hz) are significantly smaller. **B-C** Head plots of the average SSVEP amplitude at 5Hz across all 64 electrodes on the scalp averaged across participants. These head plots clearly illustrate the effect of increasing stimulus contrast on SSVEP amplitude for both dominant eye monocular and binocular conditions (**B**), and the impact of placing an ND filter in front of the dominant eye of the observer (**C**). That is, SSVEP amplitude, which is concentrated at the back of the head falls as the strength of the ND filter increases if stimuli are viewed though the filtered eye alone, but no meaningful change is observed when stimuli are viewed binocularly.

4 Modelling the Fourier Amplitude and Phase of SSVEPs

An increase in stimulus contrast leads to an increase in the amplitude of SSVEPs that is well defined by conventional models (Baker and Wade, 2017; Brown et al., 1999; Candy et al., 2001; Tsai et al., 2012; Zemon and Ratliff, 1984). Traditionally, these models operate on an input that is a scalar representation of stimulus contrast, and return a value that represents the normalized scalar response amplitude (Carandini et al., 1997; Heeger, 1992), but they can also predict the amplitude of single or multiple frequency components in SSVEPs if given a time-varying input. Here, we further extend these models to account for the temporal dynamics of SSVEPs (i.e., phase lag) by adding temporal filters to the two-stage contrast gain control model of binocular combination (Baker et al., 2008, 2007a, 2007c; Baker and Meese, 2007; Meese et al., 2006). This produces a time dependent output that allows us to model the effects of a monocular decrease in luminance on SSVEP amplitude and phase. Briefly, this model has two distinct stages of contrast gain control, one before and one after binocular combination (see **Figure 3A**). The first stage of the model includes monocular contrast gain control and interocular suppression followed by linear binocular summation, which is defined as:

$$binsum = \frac{c_L^m}{S + c_L + c_R} + \frac{c_R^m}{S + c_R + c_L} \qquad \textbf{(1)}$$

Parameters m and S were fixed and set to 1.3 and 1 respectively (Baker et al., 2007; Meese et al., 2006) while $c_{(R,L)}$ is the sinusoidal modulation of stimulus contrast presented to the observers' right (R) and left (L) eye: $c(t) = 0.5A\,(\sin(2\pi f t + \phi) + 1)$. A defines the maximum stimulus contrast, while f and ϕ are the temporal frequency (5Hz) and phase (0; respectively) of the modulation (identical to the stimulus modulation). The second contrast gain control stage is given as:

$$R_{bin} = \frac{binsum^p}{Z + binsum^q} \qquad \textbf{(2)}$$

where p, q, and Z are fixed model parameters set to 7.665, 6.5,0.1. All parameters used in the contrast gain control stages of our model were fixed at previously reported values (Baker et al., 2008; Georgeson et al., 2016).

We extend the two-stage contrast gain control model into a dynamic variant to fit SSVEP amplitude and phase values by placing a temporal filter prior to the first contrast gain control stage of the model (see **Figure 3A**). The form of the temporal filters (TF) were taken from Swanson et al., (1987), who measured temporal response functions (Watson and Nachmias, 1977) in human observers under different luminance levels. Placed prior to the first stage of contrast gain control, these filters serve to attenuate and alter the phase of the sinusoidal input (c) to the model in a biologically relevant manner. The temporal filters were formed by taking the scaled difference between two five stage impulse response functions (n = 5), $I(c,t) = (t^{n-1}e^{-2\pi ct})/(n-1)!$, with their respective corner frequencies c_1 and c_2, defined as:

$$\text{(3)} \qquad TF = A\left[\frac{I(c_1,t)}{k_1}\right] - B\left[\frac{I(c_2,t-t_0)}{k_2}\right]$$

Parameter t_0 to define the latency difference in the onset of the two filters, while k_1 and k_2 are normalization constants.

To generate SSVEP components from the model, we pass the rectified sinewave through the temporal filter and contrast gain control stages of the model. The output of the model is then Fourier transformed and the amplitude and phase values of the 5Hz component are extracted. In order to adjust the response amplitude of the model to those of our SSVEPs, we add a baseline amplitude value, set to the noise level of our EEG data (0.16μV), to the Fourier spectrum. We optimized the temporal filters to fit SSVEP amplitude and phase for each viewing condition and observer with the 5 parameters that define the temporal filter. Model fitting was completed in MATLAB with *fminsearch* to minimize the quantity

$$\text{(4)} \qquad SS_{error} = \sum_{i=1}^{n}(model_i - data_i)^2$$

The resulting model responses for each participant were then averaged across participants. We optimized parameter values for the monocular viewing condition alone, and cross-validated our parameter estimates by using these to generate binocular viewing responses and the contrast response functions measured without ND filters.

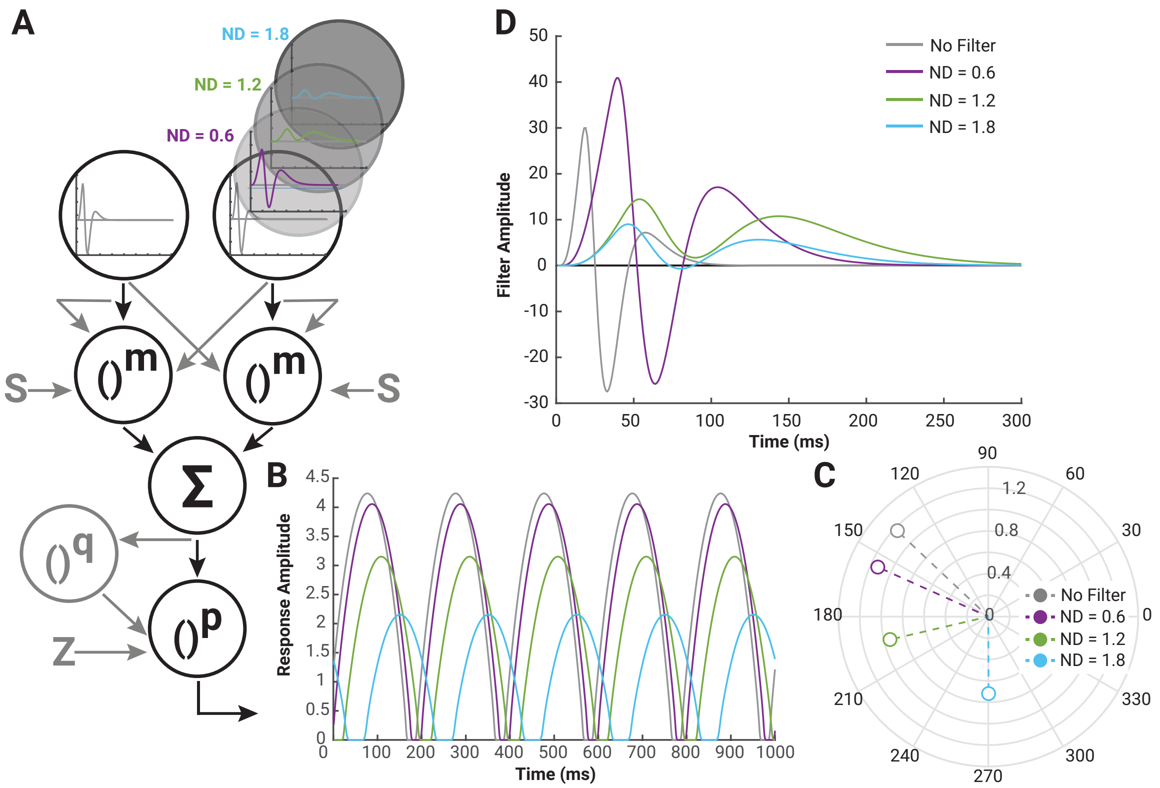

Figure 3. A The architecture of the modified two-stage contrast gain control model. ND filters are placed before the first contrast gain control stage (right eye input with ND filters of increasing strength, left eye input no ND filter). Each ND filter contains the Impulse Response Function that modulates the input to the model according to the transmittance of the filter. The temporal filters shown represent the participant average temporal filters. See text for details on the remaining model architecture. **B** The model, which receives as input a temporal waveform (5Hz) outputs a non-sinusoidal temporal waveform. **C** The waveform is then Fourier transformed and the amplitude and phase values of the 5Hz component are extract (shown in polar coordinates). The parameters of the temporal filter were fit to the human data by calculating the vector distance between the complex Fourier components at 5Hz of the data and model output. **D** The best fitting temporal filters defined by data from the monocular viewing condition for all ND filters.

5 Results and Discussion

The average SSVEP amplitude change across stimulus contrast and ND filter strength is shown in **Figure 4A** and **4B** respectively. Amplitude increased monotonically as a function of stimulus contrast, $F(4, 32) = 5.56$, $p = .002$, $\eta_p^2 = .41$, and we found no difference between SSVEP amplitude measured monocularly (dominant and non-dominant eye) or binocularly (interaction effect: $F(8, 64) = 0.58$, $p = .791$; main effect of ocularity: $F(2, 16) = 0.54$, $p = .593$). This is expected for stimuli presented at the contrast values used here (Baker & Wade, 2017; Legge, 1984) because the increased excitation from stimulating both eyes is precisely balanced by the interocular suppression between the eyes. To generate contrast response functions from our model, we use the temporal filter estimated from the no ND filter viewing condition (stimulus contrast =96% or 39.6dB) and inputted sinusoidal waveforms modulated in amplitude to represent the 5 different contrast levels used in this study. Model fits are shown as the solid lines in **Figure 4A.** While the model contrast response function could be improved, they capture the general increase in the amplitude of SSVEPs as a function of stimulus contrast well. We could have adjusted the parameters of the model to improve fits, however, we opted to keep the model parameters fixed for two reasons. First, the main goal of this manuscript is to define the decrease in neural response amplitude in response to a decrement in luminance, and not the increase in response according to stimulus contrast. Additionally, given the already large number of parameters used to define the temporal response filters (Swanson et al., 1987), we decided to keep all parameters of the two-stage contrast gain control model fixed and similar to previous implementations (Baker et al., 2008; Georgeson et al., 2016; Meese et al., 2006), and only allow the parameters of the temporal filters to vary when fitting the ND filter data.

Monocular SSVEPs to stimuli presented to the filtered eye showed a statistically significant decrease in amplitude as a function of ND filter strength, $F(3, 24) = 4.45$, $p = .013$, $\eta_p^2 = .357$, and reached noise-level amplitudes at our darkest filter (1.8ND). SSVEPs under binocular viewing were statistically significantly different from those of the monocular viewing condition, $F(1, 8) = 6.50$, $p = .034$, $\eta_p^2 = .448$). Post-hoc tests show this effect is predominantly driven by SSVEP amplitudes for a 1.8ND filter, $t(8) = -2.97$, $p = .018$, d = -1.87, 95% CI of d [-3.36 -0.31], which is in line with previous findings that have shown severe drops in monocular amplitude of ERPs and SSVEPs at filter densities near or equal to 2.0ND (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). The parameters of the temporal response functions (**equation 3)** were optimized to fit SSVEPs from the monocular viewing condition for each ND filter strength. The best fitting temporal filters (see **Figure 3D**) show a progressive drop in peak amplitude in addition to an increase latency in reaching their peak amplitude as a function of ND filter strength (from 0.6ND to 1.8ND), which captured the decrease in SSVEP amplitude found in our observers. We used the same temporal filters to generate model predictions for the binocular viewing conditions; the unfiltered eye input was adjusted by the no ND temporal filter (grey line in **Figure 3D**) and the filtered eye by the temporal filter calculated for a given ND strength under monocular viewing. Thus, binocular viewing data from the model was generated with no free parameters or additional data fitting procedures. Binocular amplitudes decreased slightly when a 0.6ND filter was placed before the dominant eye of observers and tapered off at stronger ND filters, which was well captured by our model. We note however, that these effects are not statistically significant (all *ps* > .05). A small attenuation of SSVEP amplitudes for data viewed binocularly is to be expected as the filtered eye must exert some influence on the binocular percept (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). However, given that the difference between these data points did not reach statistical significance, we are cautious to attribute the small decrease in SSVEP amplitude to the influence of the filtered eye.

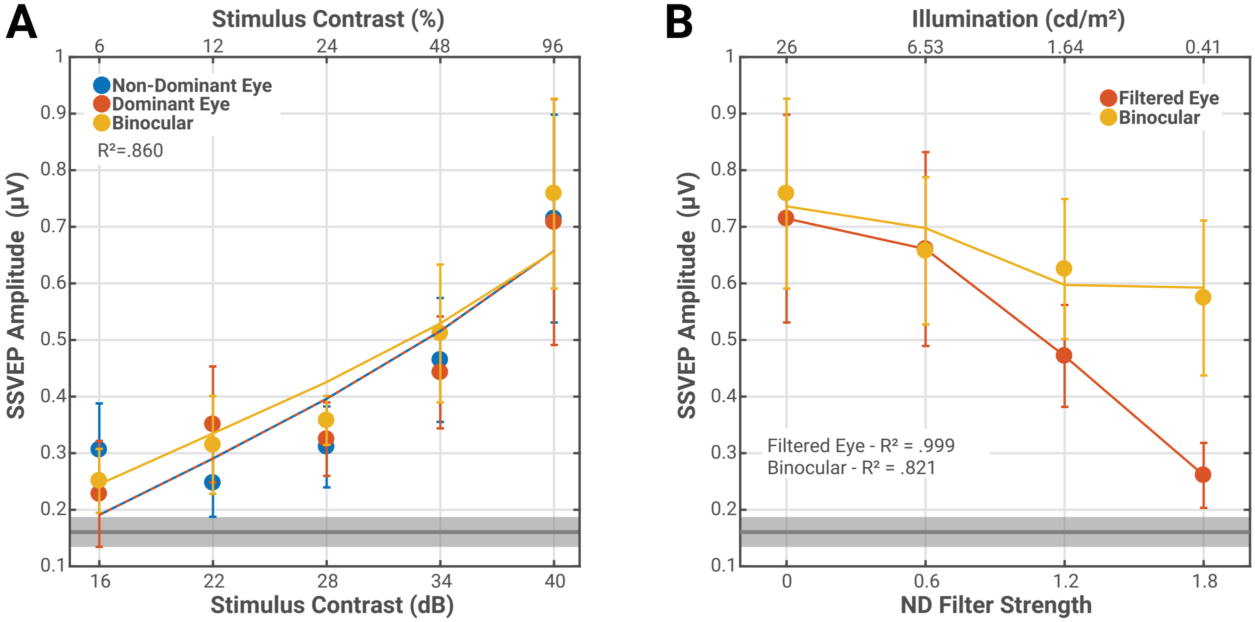

Figure 4. Averaged (N = 9) SSVEP amplitudes (µV) measured for sinusoidal gratings of varying contrast (**A** Contrast Response SSVEP Amplitude) and to gratings of 96% contrast with varying ND filter strength (**B** ND Filter SSVEP Amplitude). Values on the abscissa indicate in **A** stimulus contrast in dB (lower axis), and Michelson contrast (upper axis) and in **B** ND filter strength (lower axis) and resulting illumination for the filtered eye (upper axis). The grey line marks the baseline SSVEP amplitude recorded when no stimuli are present on the display. Error bars and grey shaded regions represent ±1 standard error of the mean. Curves represent the model predictions for SSVEP amplitude across stimulus contrast (**A**) and ND filter strength (**B**). The model output for both the dominant and non-dominant eye SSVEP amplitudes in **A** (red and blue lines) overlap perfectly as this model predicts equal sensitivity between the eyes to monocular stimuli presented at equal luminance values.

SSVEP phase angles, which are representative of a measure of the response latency of an oscillatory mechanism (Strasburger, 1987), for stimuli of varying contrast and luminance are shown in **Figure 5A** and **5B** respectively. Data are shown in polar coordinates, where the radial component depicts SSVEP amplitude (as in **Figure 4**) and the angular axis shows the Fourier phase angle (estimated response latency, inferred from the periodicity of our stimuli, are shown in parentheses in **Figure 5B**). Standard error of the cross-participant mean SSVEP amplitude and phase are represented as ellipses. The semi-major axis of the ellipse represents the standard error of the Fourier phase angle, and its semi-minor axis, that of the Fourier amplitude. As Fourier phase is a circular variable, these polar plots should be read as follows: values at or near 0 on the angular axis have a phase angle like that of the sinusoidal flicker of the stimulus (i.e., near instantaneous responses to the stimulus), while values with greater phase angles lag behind that of the stimulus flicker (approximately 16ms per 30^0 step). Fourier phase is defined modulo 360^0, thus, phase angles at low stimulus contrast — that lie near 0 — should not be interpreted to have near instantaneous response latency with the stimulus flicker, but instead phase lags that approach or are slightly greater than a full stimulus flicker cycle (i.e., response latency of 200ms).

The phase angle of SSVEPs is inversely related to stimulus contrast, $X^2(8) = 44.70$, $p < .001$, but unaffected by the viewing condition (whether stimuli are viewed monocularly or binocularly; effect of eye: $X^2(4) = 6.47$, $p = .167$, interaction effect: $X^2(8) = 6.37$, $p = .606$), which is expected in a sample of normal observers (Meese et al., 2006; Zhang et al., 2011). Response latency was shortest (100ms) for gratings of maximum contrast (i.e., 39.6dB), and increased as contrast decreased, reaching response latency values near 200ms at our lowest stimulus contrast (15.6dB). A response latency of 100ms for stimuli of high contrast corresponds well with previous EEG reports (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989), however, response latencies for lower stimulus contrast values do exceed those of previous findings, which may be attributed to their use of transient VEPs to infer latency as opposed to SSVEPs. This is because the latter includes both a pure delay of signal transmission (i.e., optic nerve transmission) and the contributions of an oscillatory mechanism (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989; Strasburger, 1987; Vialatte et al., 2010).

Response latency to our stimuli increased as luminance decreased when viewed monocularly, but was unaffected when stimuli were viewed binocularly. Monocular response lags, which represent the difference in latency between the no-filter and ND filter conditions increased proportionally to ND filter strength ($M_{0.6ND}$ = 11.49ms, SD = 31.46; $M_{1.2ND}$ = 27.99ms, SD = 41.95; $M_{1.8ND}$ = 82.99ms, SD = 40.84), and was statistically significantly different from the no filter response latency at a ND filter strength of 1.8, $t(8) = 2.03$, $p = .038$, . Binocular response lags remained near a value of 0 across all ND filter strengths, ($M_{0.6ND}$ = -3.67ms, SD = 25.80; $M_{1.2ND}$ = -6.47ms, SD = 30.90; $M_{1.8ND}$ = -15.63ms, SD = 36.94; all ps > .05). Most importantly, the increase in response latency for monocular viewing, and the absence of an effect under binocular viewing were well captured by our model. As a reminder, we only fit the parameters of the temporal filters to the monocular viewing data, and use the same filters to predict the attenuation and response latency of the filtered eye under binocular viewing. The temporal filter estimated for the monocular no filter condition was used to define the input to the unfiltered eye under binocular viewing. Thus, the input to the unfiltered eye in our model was faster and of greater amplitude than that of the filtered eye. This leads to relatively greater interocular suppression from the unfiltered eye onto the filtered eye and a binocularly summed output that is most representative of the unfiltered eye responses. The ability of our model to generate binocular response latencies that are unaffected by ND filters suggests that neural responses to dichoptic stimuli can be sufficiently explained by adjusting a temporal filter to reflect neurophysiological responses to decreasing amounts of illumination. Any additional changes to interocular interactions (as proposed by Zhou et al., 2013) are not necessary.

Figure 5. A Polar representation of the resulting SSVEP Fourier amplitude and phase from the contrast response conditions. Under all three viewing conditions shown here, SSVEP amplitude increased according to stimulus contrast, while SSVEP phase decreased (response latency shortened). Ellipse error areas represent +/- one standard error of the mean for Fourier phase (semi-major axis) and amplitude (semi-minor axis). The black line and shaded region indicate the baseline amplitude (0% contrast) and its respective standard error. The current architecture of the model is not designed to generate a change in phase angle given a change in stimulus contrast as our aim here was to define interocular interactions that result from a change in luminance, thus no model fits are presented in this chart. Values in the polar plots indicate the average response latency (standard deviation in parentheses) for each stimulus contrast. **B** Polar plots of the relative phase lags $(\theta_{ND}/\theta_{noND})$ for monocular and binocular viewing conditions. Circle markers show the observer phase lag for a given ND filter strength (with the corresponding Fourier amplitude), while square markers show the model output averaged across all participants. Response latency is presented in parentheses beneath the phase angle. Monocular response latency increases as a function of ND filter strength in comparison to that measured without an ND filter. Under binocular viewing conditions, no change in response latency is observed. Standard errors of both Fourier amplitude and phase lag are drawn as ellipses around the data point. Observer standard error is depicted by shaded ellipses, while model standard error is shown by the outlined ellipses. The grey line marks the SSVEP amplitude of the no filter condition for monocular (right) and binocular viewing (left), while the black line and shaded area indicate the baseline amplitude and its respective standard error.

6 Psychophysical Measures

An interocular imbalance in luminance induced by a ND filter will attenuate and lag SSVEPs to stimuli presented only to the filtered eye, but has little effect when stimuli are presented to both eyes. Whether these effects are representative of the observers' percept, however, must be demonstrated psychophysically. Thus, in addition to our SSVEP experiment, observers completed two psychophysical experiments that bring behavioural support to the two-stage contrast gain control model used to explain the effects described above. Additionally, we demonstrate that our model architecture is well-suited to explain not only the neural responses to stimuli presented above, but effects of monocularly decreasing luminance on psychophysical performance. Participants completed two psychophysical paradigms that have previously been used to measure the hindrance of an interocular imbalance in luminance on performance: a binocular summation experiment (Baker et al., 2007b) and a binocular rivalry experiment (De Belsunce and Sireteanu, 1991; Leonards and Sireteanu, 1993). Performance on these tasks is known to be subject to interocular interactions, and thus, any behavioural change attributed to the ND filter in these paradigms further supports the suppressive effects of binocular vision on delayed monocular signals we defined above. We implement the model in the binocular summation experiment, but present only the psychophysical findings of our binocular rivalry experiment, as the dynamic properties of binocular rivalry would require too large a change to our modelling architecture, and add no further insight to our findings.

6.2 Binocular Summation

6.2.1 Stimulus and Procedures

Stimuli were 3 cycles/° horizontal sinusoidal gratings windowed by a raised cosine envelope to subtend 5° of visual angle on the retina (identical to those of the SSVEP study). Monocular and binocular contrast detection thresholds were measured with a 2-AFC staircase procedure (3-down, 1-up), which adjusted contrast in logarithmic steps around threshold (step-size = 3dB; see Baker, Meese, Mansouri, et al., 2007). On any given trial, observers were first presented with a blank screen and fixation cross in the centre of the display for 500ms. Two 200ms intervals were presented in succession, interlaced by a blank screen for 400ms; one interval contained the stimulus, while the other was blank. Like in the SSVEP experiment, target contrast was temporally modulated according to a full cycle of a raised sinusoidal waveform during the stimulus interval: contrast began at 0%, and increased to 100% of its nominal maximum, and return to 0% over a period of 200ms. Observers were asked to indicate which of the two stimulus intervals contained the target. The onset of a stimulus interval was paired with a tone to minimize observer uncertainty. Contrast detection thresholds were determined by Probit analysis, and taken to be the 75% correct point on the fitted function.

There were nine conditions in this study: contrast detection thresholds of the non-filtered eye were only measured once, while the filtered eye and binocular conditions were each repeated four times (no filter, and at all three ND filters levels). As in the EEG portion of this study, observers completed the no filter conditions before repeating the experiment with ND filters. This ensures that observers were dark adapted when measuring detection thresholds under low illumination levels. Observers completed three staircases per condition, which were subsequently combined to estimate thresholds.

6.2.2 Results and Discussion

Average monocular and binocular contrast detection thresholds (CS) and summation ratios ($SR = CS_{Binoc}/CS_{Monoc(Non-Dominant)}$) for all ND filter strengths are shown in **Figure 6A**. Binocular summation—with no filter placed before the non-dominant eye—was approximately linear (SR = 2), slightly higher than the typically reported ratios of 1.4 - 1.8 (Baker et al., 2007c; Blake et al., 1981; Campbell and Green, 1965; Legge, 1984b; Meese et al., 2006; Meese and Baker, 2013). We found that attenuating the responses of a stimulus by reducing its luminance with ND filters decreased the binocular advantage and reached monocular performance levels at dense ND filters. This is expected when measuring contrast detection thresholds as the relative sensitivity of each eye influences binocular contrast sensitivity (Baker et al., 2007b; Nes et al., 1967). However, binocular contrast sensitivity never fell below that of the monocular contrast sensitivity from the unfiltered eye, suggesting minimal or no binocular inhibition from difference in luminance between both eyes (i.e., we find no evidence of Fechner's paradox in our subjects; Gilchrist and Pardhan, 1987).

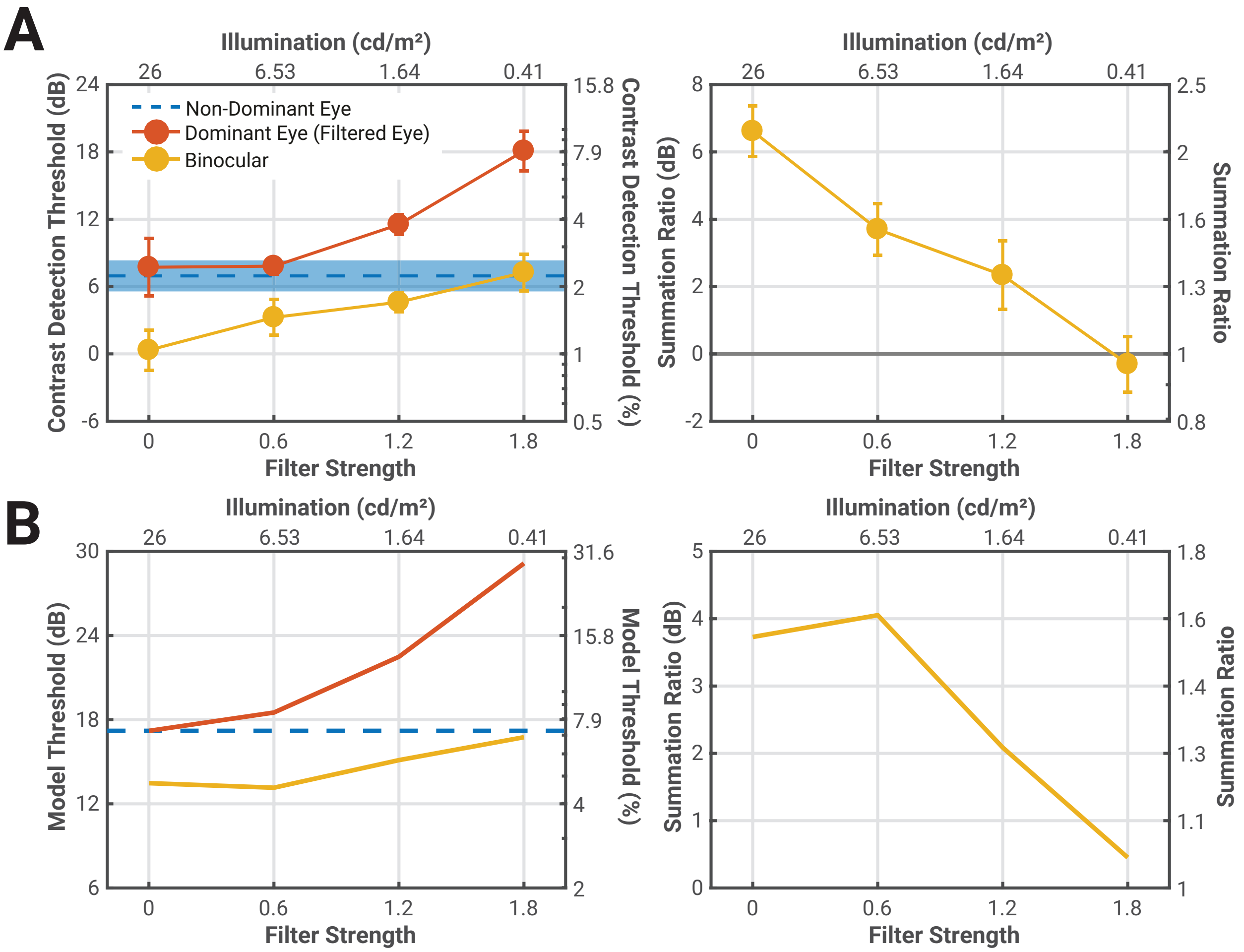

Figure 6. (A) Contrast detection thresholds (left) measured monocularly and binocularly, and binocular summation ratio (right) across all ND filter conditions of this study. Contrast detection thresholds for the non-dominant eye were only measured at baseline (no filter), and are drawn as a line across all ND filter values for reference. Error bars represent +/- 1 standard error of the mean (error for the non-dominant line is represented as a shaded region). Summation ratios decreased as a function of filter density, and reached monocular levels (no summation) for filters of 1.8ND. **B** Model predictions of monocular and binocular contrast detection thresholds across all ND filter conditions (Left). Model thresholds were generated by feeding inputs varying in contrast, and selecting an arbitrary cut-off value (k = 1) that indicated target detection. While the threshold values generated by the model do not match human observer thresholds, the influence of the ND filter on target detection is captured well by the temporal filters we estimated from our EEG data. (Right) The model summation ratios across the ND filter conditions. The decrease in summation as a function of ND filter strength is well captured by the model. However, it is incapable of capturing the unusually large summation ratio we obtained with no ND filters.

Binocular summation is well described by physiological summation – the linear combination of normalized monocular signals (Baker et al., 2007b; Georgeson et al., 2016; Meese and Baker, 2011). This is a fundamental component of our model as it defines the impeding effects of ND filters on the amplitude and phase of SSVEPs. It thus follows that our general model architecture should also be able to account for the psychophysical binocular summation data collected here. We do not attempt to fit the model parameters to the binocular summation data shown here, but instead feed the EEG model with a single cycle of a sinusoidal waveform of varying amplitude (to simulate different stimulus contrast values), identical to the psychophysical procedures of this study. The effects of the ND filter were modelled with the temporal filters of the EEG study. To generate contrast detection thresholds (C_t) from our model response (i.e., amplitude), we selected an arbitrary model criterion value ($k = 1$) to determine predictions for which

$$k = resp(C_t). \qquad \textbf{(5)}$$

The model predictions are shown in **Figure 6B**. While the model detection thresholds do not match those of human observers in magnitude, they do in kind. The model predicts a similar increase in threshold for both the monocular and binocular viewing conditions as a function of the ND filter strength, and consequently, a decrease in binocular summation that mirrors – in the ND filter conditions - that of our human observers, reaching monocular levels of summation at an ND filter of 1.8.

An interesting observation with this model type is that the binocular summation ratio (the ratio of binocular to monocular contrast detection thresholds) is given by $2^{1/m}$ = 1.7 or 4.6dB when *m* is set to 1.3 (Baker et al., 2007a). While this approximates binocular summation well in most cases, binocular summation with no ND filter was unusually high in our sample: the baseline binocular summation ratio was greater than the typically reported value and quasi-linear (SR = 2.14 or 6.61dB). A summation ratio this high is uncommon and it is plausible that the filtered eye of our observers was strengthened by the ND filter in studies conducted prior to the summation study (e.g., the EEG experiment), as short monocular deprivation (or partial occlusion) is known to increase the contribution of the filtered eye to the binocular percept (Zhou et al., 2013). However, it is difficult to ascertain how much influence this may have had on our quasi-linear summation ratio as monocular deprivation requires a substantially longer occlusion period (~2.5 hours) than that undergone by our observers in the experiment preceding this one (12 minutes with filters in the EEG experiment). We also find no difference in monocular contrast sensitivity between the filtered and unfiltered eye with no ND filter that would be indicative of a strengthening of the filtered eye by ND filters (see **Figure 6**). As we do not attempt to fit the responses of the model to the binocular summation data by adjusting the *m* parameter, and keep it set to 1.3, our model is incapable of generating binocular summation with no ND filter as high as that of our human observers. Nevertheless, we demonstrate here that the model architecture we have created to describe the changes in SSVEP amplitude and phase values when luminance is imbalanced between both eyes can also capture general changes in psychophysical measurements of binocular summation. The data and model predictions further demonstrate how a severe luminance imbalance between the eyes can make a system appear monocular, despite having a binocular architecture.

6.3 Binocular Rivalry

6.3.1 Stimulus and Procedures

Stimuli were two 3 cycles/° oblique (45° and 135°) sinusoidal gratings windowed by a raised cosine envelope to subtend 5° of visual angle on the retina. Dichoptic presentation of both gratings (45° to the right, 135° to the left) was accomplished with the same stereo shutter goggles as described above (see **Figure 7A**; apparatus was identical to that of the SSVEP study). Stimuli were presented at the centre of the display for a duration of 60 seconds, during which observers continuously indicated the orientation of the perceptually dominant grating via button press. All participants completed the rivalry task four times, once without an ND filter in front of the dominant eye, and then once for each ND filter strength (filter strength order was counterbalanced across observers).

6.3.2 Results and Discussion

Under normal binocular viewing, we find a small dominant eye effect of rivalry. The stimulus presented to the dominant eye of the observer was perceived approximately 25% more often than that of the non-dominant eye (ln(ratio) = 0.17, $SD_{\ln(\text{ratio})}$ = 0.32, *logit d* = .121), an effect often found in binocular rivalry studies (Bartels and Logothetis, 2010). Importantly, the proportion of dominance events in the filtered eye fell rapidly as a function of ND filter strength. Perceptual dominance of stimuli presented to the filtered eye occurred half as often as those of the unfiltered eye with a 1.8ND filter (ln(ratio) = -0.67, $SD_{\ln(\text{ratio})}$ = 0.37, *logit d* = .336; see **Figure 7B**). The duration of dominance events in the filtered eye also decreased as a function of ND filter strength. The histograms in **Figure 7C** show distributions of dominance durations (pooled across all observers) for each eye at the four ND filter strengths. At baseline and with a 0.6ND filter, the distributions of dominance events of each eye overlap significantly (no filter: KS = 0.133, *p* = .424; 0.6ND: KS = 0.181, *p* = .076). As the strength of the ND filter is increased, dominance events in the filtered eye decreased in duration, which shifted the distribution towards the left while that of the unfiltered eye remained unchanged (1.2ND: KS = 0.252, *p* = .004; 1.8ND: KS = 0.598, *p* < .005). Unlike our SSVEP and binocular summation data, we chose not to model the effects of ND filters on the number of dominance events and dominance duration in our binocular rivalry data. There exist models of binocular rivalry that are structurally similar to the psychophysical model we present here (Wilson, 2007, 2003), but their implementation would have necessitated significant changes to the model architecture in addition to a series of additional parameters that define the complex dynamics of binocular rivalry that go beyond the goals of this manuscript.

A decrease in the number of dominance events and their duration across filter strength is similar to findings of binocular rivalry in observers with poor binocularity (e.g., amblyopia; De Belsunce & Sireteanu, 1991), and corroborate previous findings that used similar methodology (Leonards and Sireteanu, 1993). Additionally, these findings clarify the influence of the ND filter on the binocular summation of monocular signals that differ in luminance. It is thought that binocular rivalry is driven, in part, by interocular competition whereby one eye will temporarily exert greater suppression on the other, resulting it its perceptual dominance (Nichols & Wilson, 2009; Wilson, 2003). As the suppressive signals from the dominant eye subside (due to adaptation; Wilson, 2003, 2007), the other eye begins to exert a larger suppressive signal and becomes dominant, and this process repeats until the stimuli are removed or can be binocularly fused. We show here that reducing the luminance input to one eye (while maintaining contrast) alters the oscillations in perceptual dominance observed in rivalry as the filtered eye's signal becomes too weak to exert any meaningful influence on the responses of the unfiltered eye. The imbalance of interocular suppression from decreased illumination thus seems a likely candidate as a mechanism that generates the changes in SSVEP amplitude. That is, the amount of suppression received by the filtered eye from the unfiltered eye in rivalry is directly proportional to the attenuation of signal input, a finding congruent with our SSVEP results and model.

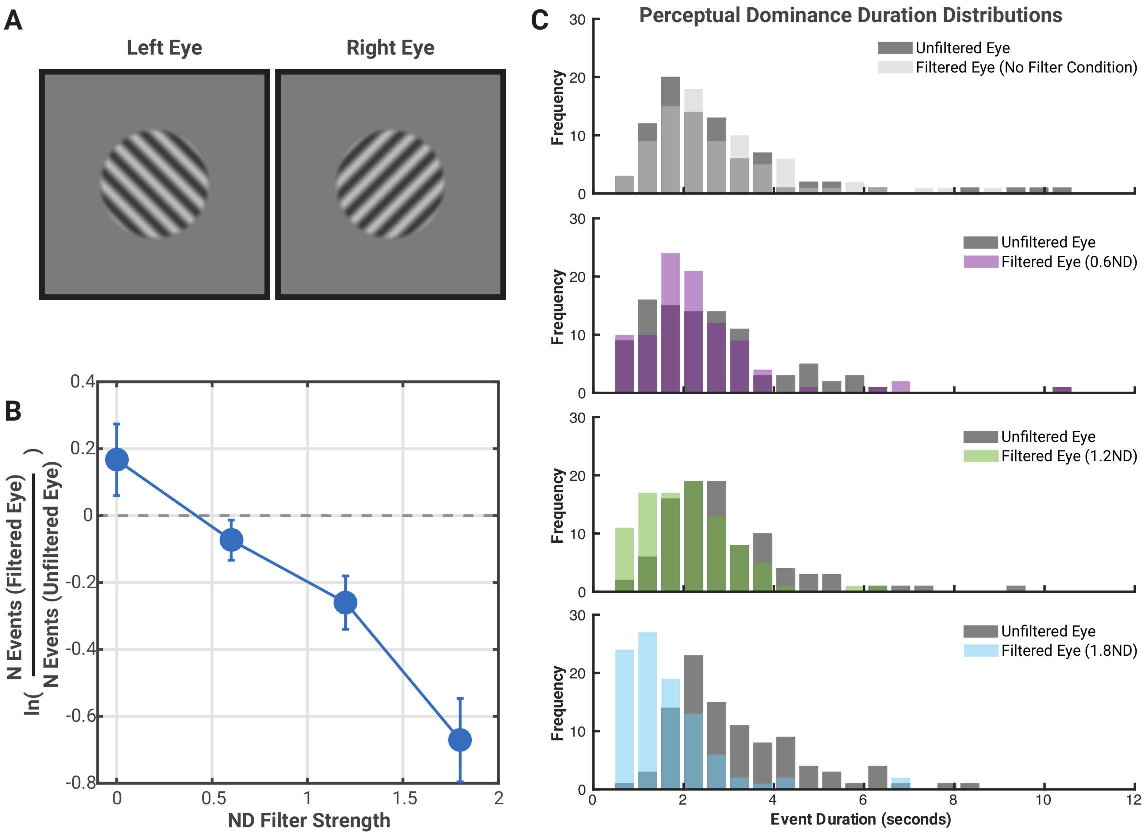

Figure 7. A Stimuli presented to observers in the rivalry task. **B** Proportion of dominance events across filter strengths. Proportion scores have been log transformed, and thus a ratio of 1 (no difference in the number of dominance events experienced by both eyes) is equal to a value of 0. Error bars represent +/- 1 standard error of the mean. **C** Dominance duration histograms for dominance events in the filtered (coloured) and unfiltered (gray) eye for all ND filter conditions. Event durations were collapsed across all observers (N = 9) to make the histograms. The duration of dominance events in the filtered eye decreased in proportion to the strength of the ND filter, leading to a leftward shift in the distribution.

7 Discussion

An imbalance in luminance between the eyes has a detrimental effect on psychophysical performance for a series of binocular tasks (Baker et al., 2008; Chang et al., 2006; Gilchrist & Pardhan, 1987; Zhou et al., 2013), which is related to the decreased amplitude and slowed onset of responses in early visual pathways under reduced illumination (Heravian-Shandiz et al., 1991; Katsumi et al., 1986; Spafford & Cotnam, 1989; Wilson & Anstis, 1969). Interestingly, a dichoptic decrement in luminance only impacts neural responses to stimuli presented to the filtered eye alone (i.e., monocular), while responses to binocularly presented stimuli suffer little from the impoverished input from the filtered eye. The unaltered responses to binocularly viewed stimuli are thought to represent the influence of interocular interactions, which suppress the delayed and attenuated signal from the darkened eye. We tested this proposed architecture, which is like that defined by Meese et al. (2006), with SSVEP and psychophysical data measured whilst observers wore ND filters of varying transmittance before their dominant eye. We find that placing biophysically plausible temporal filters prior to the first contrast gain control stage is sufficient to account for the attenuation and lag generated by the ND filter.

Our study replicates earlier findings that the darkening of stimuli with progressively stronger ND filters leads to a decrease in SSVEP amplitude and lag in the SSVEP phase when stimuli are presented monocularly (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). SSVEP amplitudes decreased as filter strength increased, reaching noise levels at a filter strength of 1.8ND, comparable to amplitudes measured from other studies with filter strengths that exceed 1.2ND (previous studies used a 1.0 and a 2.6ND filter and we thus estimate the magnitude of their effects at our ND filter levels; Heravian-Shandiz et al., 1991; Spafford & Cotnam, 1989). Response latency in the filtered eye increased according to filter strength, generating progressively greater asynchronies between the response latency of the filtered and unfiltered eyes. The increase in response latency recorded here was greater than those of previous reports, which have typically found delays of approximately 35ms for ND filter strengths of 1.5ND (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). While response latency measured with steady-state measures are generally greater than those measured with ERPs (Strasburger, 1987; Vialatte et al., 2010), one other study has estimated response latency from the phase component of steady-states (e.g., SSVER in MEG) of 38ms with a 1.5ND filter (Chadnova et al., 2018*)*. However, methodological differences including the type of stimulus (sinusoidal gratings VS noise), absolute (mean) luminance, and stimulus contrast (96% VS 32%) can account for the differences in findings between studies. Importantly, previous studies found, as we did, no change in the response latency in binocular viewing conditions, which suggest this viewing condition is not affected by the temporal asynchrony generated with an ND filter (Gilchrist and Pardhan, 1987; Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989).

We do observe a small decrease in SSVEP amplitudes that levelled-off at a filter strength of 1.2ND in our binocular viewing condition. While this effect was not statistically significant, the small decrease is congruent with previous reports of a mild drop in neural response amplitude to binocularly viewed stimuli when the luminance in one eye is decreased (Heravian-Shandiz et al., 1991; Spafford and Cotnam, 1989). These effects may be attributed to a slight disruption in binocular summation from the attenuated and asynchronous input from the filtered eye. Indeed, binocular contrast sensitivity was evidently affected by the monocular decrease in luminance, which impeded binocular summation. That said, the decrease in SSVEP amplitude for binocularly viewed stimuli was significantly milder than that of binocular summation. This is to be expected as binocular summation is most evident when measured at contrast detection threshold while our SSVEP study presented sinusoidal gratings set at 96% contrast (Meese et al., 2006; Meese and Baker, 2011). It is also important to caution any direct interpretation between neural and psychophysical responses: SSVEP amplitude can be highly correlated with observer percept (Norcia et al., 2015), but are by no means a direct representation of percept (Timora and Budd, 2013). Multiple factors that contribute to an observers' contrast detection thresholds that are not necessarily measurable with SSVEPs (e.g., decision criteria). Still, it is likely the summation of monocular signals will be impeded by a difference in luminance even when stimuli are presented well above contrast detection thresholds, albeit to a milder extent (Meese et al., 2006; Meese and Baker, 2011).

We postulated that a mechanism that maintains normal signal transmission under our binocular viewing conditions can be described by a standard binocular summation model that adaptively suppresses the delayed and attenuated signal via interocular suppressive terms (Baker et al., 2008; Meese et al., 2006), and found this model described the effects of an ND filter on the neural and psychophysical data well. The only addition brought to this model architecture were biophysically plausible temporal filters prior to the monocular contrast gain control stage to fit the time sensitive SSVEP data. These temporal filters adjusted the magnitude of input for a given ND filter strength according to a set of biophysically relevant parameters defined by Swanson et al. (1987) for different illumination conditions. The model generated normal signal transmission regardless of ND filter strength when stimuli were viewed binocularly as the faster onset of the no filter temporal filter ensured it took precedence over the slower filters of the ND conditions when the inputs from both eyes were linearly summed. This adjustment to our model is a temporal variant of an attenuation parameter that decreases the value of the input to one eye, while leaving all other properties of the binocular summation model intact (Baker et al., 2008). Response attenuation is known to describe various psychophysical effects in observers with poor binocularity, including dichoptic masking and binocular summation (Baker et al., 2008, 2007b). Here, we demonstrate how to extend response attenuation to become time sensitive, and further, showed that normal interocular interactions paired with response attenuation are sufficient to account for the stability of response latencies under binocular viewing by adaptively suppressing the attenuated and delayed responses from the filtered eye (Baker et al., 2007b; Sengpiel et al., 1995; Zhou et al., 2013). That said, our modelling approach does not preclude the use of additional or weighted suppressive terms (Baker et al., 2008; Huang et al., 2011; Zhou et al., 2013), the inclusion of other temporal filters between the monocular and binocular summation stages (Cunningham et al., 2017), or any increments in additive internal noise from a reduction in luminance (Li et al., 2015; Pelli, 1990). However, the ability of our model to mirror the response patterns measured with two different paradigms (EEG and psychophysics) suggests it is unnecessary to include any additional parameters to improve model fit. It may be of future interest to verify how the different approaches to the combination of monocular responses fare in comparison to the model defined here.

7.1 Conclusion

The amplitude and onset of neural responses to visually presented stimuli is subject to illuminance: under low luminance conditions, neural responses show increased lag and decreased amplitude proportional to the decrement in luminance to the eye (Gilchrist and Pardhan, 1987; Heravian-Shandiz et al., 1991; Heron and Dutton, 1989; Hess et al., 1980; Morgan and Thompson, 1975; Spafford and Cotnam, 1989). If stimuli are presented binocularly, the impact on neural responses is mild: response amplitude may show a small decrement, while response phase will remain mostly unchanged relative to their baseline (no filter) counterparts. While the effects of an imbalance in luminance between both eyes has been well-described with psychophysical and neurophysiological measures, less is known about the underlying mechanism responsible for these effects. We postulate that a binocular summation model (Meese et al., 2006), which linearly combines the normalized input from each eye (with interocular suppression) prior to a second normalization stage, would be able to maintain normal signal transmission under binocular viewing when monocular responses are asynchronous and differ in amplitude. Our model was able to fit both our neural (SSVEPs) and psychophysical data well, indicating that simple response attenuation is sufficient to generate the monocular and binocular response patterns that occur under different monocular illumination conditions. Our findings may offer insight on future clinical studies that measure binocular function in individuals with poor binocularity. That is, if attenuation alone contributes to monocular deficits (as observed here), then ND filters can serve as an adequate simulation tool to replicate the visual deficits in individuals with poor binocularity (e.g., amblyopia; Harrad et al., 1996; Sengpiel, 2014). This has already been proposed with psychophysical findings (see Baker et al., 2008), and it would be interesting to conduct a similar study to ours in a sample of individuals with amblyopia. This could serve to 1) verify whether they resemble our normal observers wearing an ND filter before their dominant eye; and 2) whether placing an ND filter in front of their fellow fixing eye of amblyopes could equate the amplitude and response latency between the eyes, similar to previous psychophysical findings (De Belsunce and Sireteanu, 1991).

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