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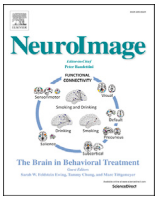

Binocular vision adaptively suppresses delayed monocular signals

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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.

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 et al., 2008, 2007b; Chang et al., 2006; De Valois et al., 1974; Gilchrist and Pardhan, 1987; Leonards and Sireteanu, 1993; Zhou et al., 2013a,b). 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 number 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 et al., 2007b; Campbell et al., 1973; De Belsunce and Sireteanu, 1991; Heravian-Shandiz et al., 1991; Leonards and Sireteanu, 1993; Zhang et al., 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 et al., 1986; Spafford and Cotnam, 1989; Wilson and 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

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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 80 ms and a 50% decrease in response magnitude in the darkened eye (Chadnova et al., 2017; Heravian-Shandiz et al., 1991; Spafford and 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. (2017) 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., 2013b). 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., 2013b). 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., 2017; 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 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.

Methods

Participants

Nine observers (2 males: authors BR and DHB), with normal or corrected to normal visual acuity participated in this study ($M_{\text{age}} = 25$ 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.

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.

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 Fig. 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