Different rules for binocular combination of luminance in cortical and subcortical pathways

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Abstract

Introduction

Binocular combination provides a higher visual sensitivity than monocular viewing. This superiority is known as binocular summation and is defined by the binocular summation ratio (BSR), which was originally believed to be around $\sqrt{2}$ (≈ 1.4) for grating stimuli at detection threshold (Campbell and Green, 1965). In other words, a monocular stimulus can elicit the same response as a binocular stimulus if it has a contrast that is 1.4 times higher. This led Legge to develop a widely accepted explanation that used quadratic summation to describe binocular combination (Legge, 1984): monocular signals from the right (R) and the left (L) eyes are squared before being summed together and the binocular response (B) is given by the square root of the output (B = $\sqrt{R^2 + L^2}$, when R and L are equal to 1, the output is $\sqrt{2}$). However, subsequent research has shown that these explanations are not fully adequate to account for binocular summation. Both of these accounts constitute single channel models, and this type of model has been shown to not being able to account for contrast detection in the presence of noise (Anderson and Movshon, 1989). Moreover, more recent research has shown that the summation ratio can vary greatly between $\sqrt{2}$ and 2 depending on factors such as the spatial and temporal frequency of a stimulus or the sensitivity difference between the eyes (Baker et al., 2018). These observations led to the development of multistage gain control models, which combine binocular summation and interocular suppression, and can account for contrast matching, detection and discrimination for spatial contrast (Ding and Sperling, 2006; Meese et al., 2006). In general, it seems that the mechanisms behind binocular combination have been thoroughly studied, as have been the anatomical pathways behind it: light enters the eye though the pupil and signals are sent from the left and right retinae to the primary visual cortex, remaining anatomically isolated while passing through the lateral geniculate nucleus (LGN) until they reach V1, where they are binocularly combined (Purves et al., 2008). However, there is an eye component that is often underestimated in its role to determine the quality of visual information: the pupil. The pupils are openings found in the centre of the eyes that appear to be black and allow light to enter the eyes. Their size determines how much light will reach the retina and it is usually determined by the ambient levels of light: in brightness the pupils will constrict and in darkness they will dilate. This is known as the pupillary light response (PLR). The anatomical pathways that regulate this response are well understood and are very clearly and extensively described in the literature (Angée et al., 2021; Mathôt, 2018; McDougal and Gamlin, 2010; Wang and Munoz, 2015). However, they are anatomically distinct from the LGN-V1 pathway meaning that binocular combination occurs separately in anatomically distinct pathways. Given this, not much is known about the computational processes behind the PLR except for some evidence of binocular interaction. The presence of a consensual response in one eye when the other is being stimulated, and the presence of convergence (one pupil responds to illumination in either retina) and divergence (both pupils respond to illumination of one retina) (Wyatt and Musselman, 1981) are evidence of this binocular interaction. With this in mind we designed an experiment that simultaneously recorded electrophysiological and pupillometric responses to investigate the combination of flickering light signals in both the visual cortex and the pupils. The results should offer new insight about basic neural circuits and information on how they might be affected in clinical disorders of vision (e.g. amblyopia). Based on previous literature, we expected to find a non-linear combination of the responses in visual cortex, as described by the gain control mechanisms, and a more linear combination of the responses and a greater binocular response at the level of the pupils. To follow up on the results that we obtained, we decided to perform a contrast matching experiment to investigate whether perception of flickering light is consistent with the results observed in the cortical pathways (visual cortex) or the subcortical pathways (pupils). Matching is a paradigm in which the perceived brightness of a standard stimulus is matched to that of a target stimulus. In the latter, the interocular ratios of luminance are varied to obtain an equibrightness curve. Previous literature has used this paradigm to investigate the binocular fusion of static stimuli and the temporal combination of spatial flickering of spatial increments (a bright target on a dark background) and decrements (a dark target on a bright background) (Anstis and Ho, 1998; Levelt, 1965). For spatial increments, it was found that binocular fusion seems to follow approximately linear combination rules. This means that, for a monocular stimulus to elicit the same response as a binocular stimulus, the former needs to have twice the signal of the latter. On the other hand, spatial decrements follow a winner-takes-all pattern. This means that the observer is seeing what the eye that is receiving the strongest signal is seeing. Our experiment used different stimuli than the ones used by Anstis and Ho: in the binocular fusion experiment, their stimuli were not flickering and, in the flicker experiment, they were always shown in both eyes. In our experiment, in some conditions, the flicker was shown to only one eye. Moreover, they were looking at the temporal fusion of the flicker while we focussed on the binocular fusion of the flicker. Based on this and on the results from our first experiment, we expected to find a near linear summation of the responses.

Methods

Participants

Thirty, twelve and ten participants were recruited for experiment 1, 2 and 3 respectively. All participants had normal or corrected to normal binocular vision. All participants gave written informed consent.

Apparatus & Stimuli

The stimuli were two discs of flickering light with a diameter of 3.74 degrees, presented on a black background. The same stimuli were used for all three experiments. Four dark red lines were added around both discs to help with their fusion into one binocular disc. Figure 1 shows an example of the of the unfused stimuli. The discs were viewed through a four-mirror stereoscope, which used front silvered mirrors and so did not suffer from internal reflections, and allowed participants to see only one fused disc. The use of a stereoscope allowed us to display the stimuli in three different ocular configurations: monocular, binocular, and dichoptic. All stimuli were displayed at a mean luminance of 42 cd/m^2 on an Iiyama Vision Master™ Pro 510 display (800 x 600 pixels, 60 Hz refresh rate), which was gamma corrected using a Minolta LS-110 (Minolta Camera Co. Ltd., Japan). For experiments 1 and 2, the stimuli were presented using Psychopy (v3.0.7). For experiment 3, the stimuli were presented using Psychopy (v2022.1.1). EEG data were collected for experiments 1 and 2 sampled at 1 kHz using a 64-electrode ANT WaveGuard cap and the signals were recorded using the ASA software (ANT Neuro, Hengelo, NL, United States). Pupillometry data were collected only for experiment 1 using a binocular Pupil Core eye-tracker (Pupil Labs GmbH) running at 120 Hz and the signals were recorded with the Pupil Capture software (Pupil Labs GmbH).

Procedure

Before each experiment, participants calibrated the stereoscope by adjusting the angle of the mirrors. This was done so that they would perceive the two discs as one fused disc when looking at the screen through the stereoscope.

Experiment 1

The experiment was conducted in a windowless room, in which the only light source was the monitor. The participants sat at 99 cm from the monitor and their viewing distance through the stereoscope was 107 cm. The experiment was carried out in one session lasting 45 minutes in total, divided in three blocks of 15 minutes each. In each block, there were 60 trials in total lasting 15 seconds each (12s of stimulus presentation, with an interstimulus interval of 3s). The participants had no task and were asked to look at the fixation crosses in the middle of the two discs while trying to minimise their blinking during the presentation period. The discs flickered in counterphase at 2 Hz, but in some conditions (cross-frequency conditions) one of the two discs flickered at 1.6 Hz. They were set at five temporal contrast levels relative to the mean luminance: 6, 12, 24, 48 and 96 %. As already stated, the mirror stereoscope allowed the use of three different ocular configurations. In the monocular configuration, one disc was set to flicker either at 2 Hz or 1.6 Hz for each contrast level, while the other disc remained stable at a constant mean luminance. In the binocular configuration, both discs flickered at the same contrast level with both discs flickering at 2 Hz in the same-frequency condition, while, in the cross-frequency condition, one disc flickered at 2 Hz and the other at 1.6 Hz. Finally, in the dichoptic configuration, one disc flickered across all contrast levels and the other flickered at a fixed contrast level that was set at 48 %. Similar to the binocular configuration, the dichoptic configuration was divided in same-frequency and cross-frequency conditions.

Experiment 2

The conditions were similar to experiment 1 (windowless room and viewing distance of 107 cm). Like in experiment 1, participants had no specific task other than looking at the fixation crosses and minimising their blinking. Unlike the first experiment, only one contrast level was used (96 %) and the discs were set to flicker at five different frequencies (2, 4, 8, 16 and 30 Hz). Only two ocular configurations, monocular and binocular, were used, with the latter having both discs flickering at the same frequency. The experiment was carried out in one session lasting 25 minutes in total, divided in five blocks of 5 minutes each. In each block, there were 20 trials in total lasting 15 seconds each (12s of stimulus presentation and 3s of interstimulus interval).

Experiment 3

The experiment was conducted in a room with a blacked-out window. The sitting and viewing distances of the participants were similar to the two previous experiments. As this was a psychophysical task, no EEG or pupillometry data were collected for this experiment. A two-interval forced-choice staircase procedure was used to collect data. In one interval, participants were presented with a standard fused disc that flickered at a set contrast level (either 24 or 48 %), which was selected by the experimenter at the beginning of each block. In a separate interval, a target fused disc flickering at varying contrast levels was displayed. The contrast level of the target was controlled by a 1-up, 1-down staircase moving in logarithmic (dB) steps of contrast. The ratio of flicker amplitudes in the left and right eyes was varied across blocks and was set to be 0, 0.25, 0.5, 0.75 or 1. The standard and the target fused discs were displayed for 1 second each, with an interstimulus interval of 0.5 seconds. After the discs appeared on screen, the participants had to indicate which interval they perceived as having the more intense flicker. The intervals were randomly ordered, and all discs flickered at a frequency of 2 Hz. Due to its long duration (162 minutes in total), the participants completed the experiment across multiple sessions divided at their own discretion. The experiment was divided in 54 blocks (3 repetitions $\times$ 2 standard contrasts $\times$ 9 target ratios), which lasted on average 3 minutes each (depending on the response speed of the participant). In each block, there were a total of 50 trials. We pooled the data from all repetitions of a given condition and fitted a cumulative normal psychometric function to estimate the point of subjective equality at the 50 % point.

Data analysis

EEG data were converted from the ANT-EEProbe format to a compressed csv text file using a custom Matlab script and components of the EEGlab toolbox (Delorme and Makeig, 2004). The data for each participant were then loaded into R for analysis where a ten-second waveform for each trial at each electrode was extracted. Fourier transform was calculated for each waveform, and the spectrum stored in a matrix. All repetitions of each condition were then averaged for each electrode. They were then averaged across the four occipital electrodes (POz, Oz, O1, O2), to obtain individual results. Finally, these were averaged across all participants to obtain the final results.

Results

Experiment 1

The results from the first experiment are shown in figures 2 and 3. Each curve is showing the amplitude of the signal for the three different configurations (monocular, binocular and dichoptic).

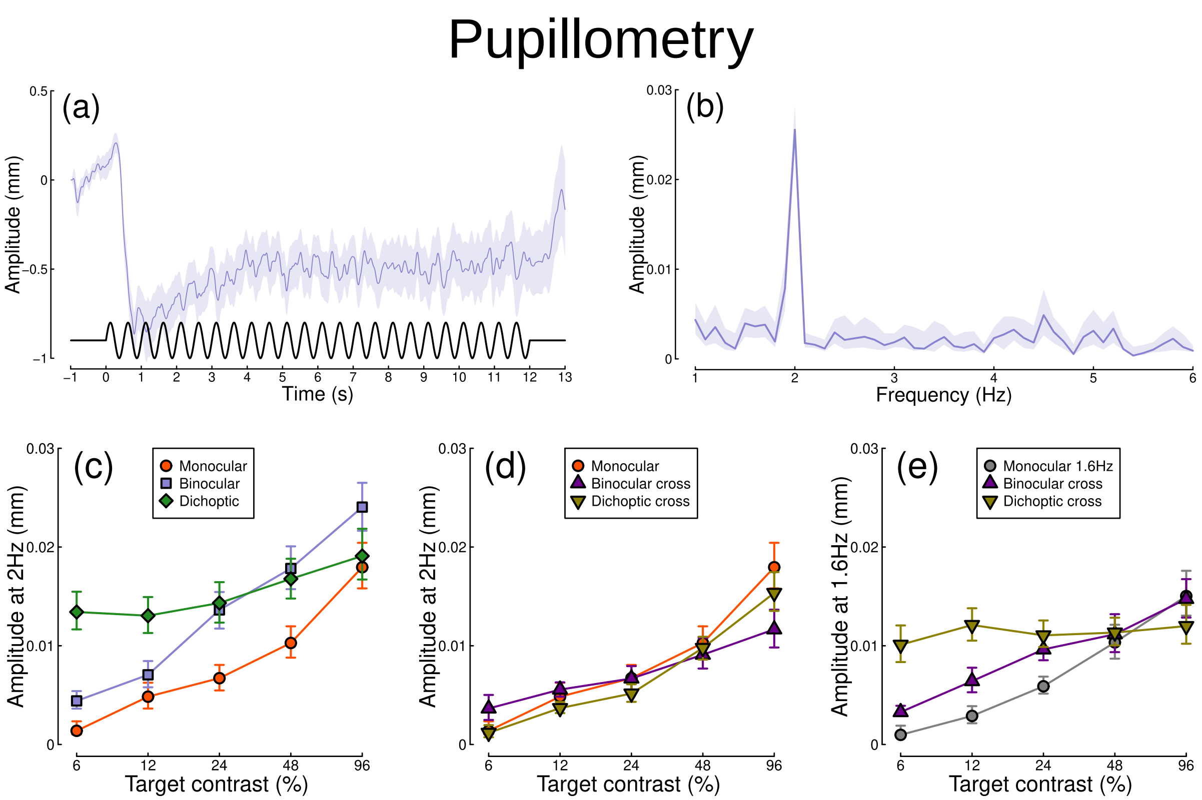

Figure 1: Summary of pupillometry results for N=30 participants. Panel (a) shows a group average waveform for binocular presentation (low pass filtered at 5Hz), with the driving signal plotted at the foot. Panel (b) shows the average Fourier spectrum. Panels (c,d) show contrast response functions at 2Hz for different conditions. Panel (e) shows contrast response functions at 1.6Hz for three conditions. Shaded regions and error bars indicate bootstrapped standard errors.

Figure 1@ref(fig:pupildata)a

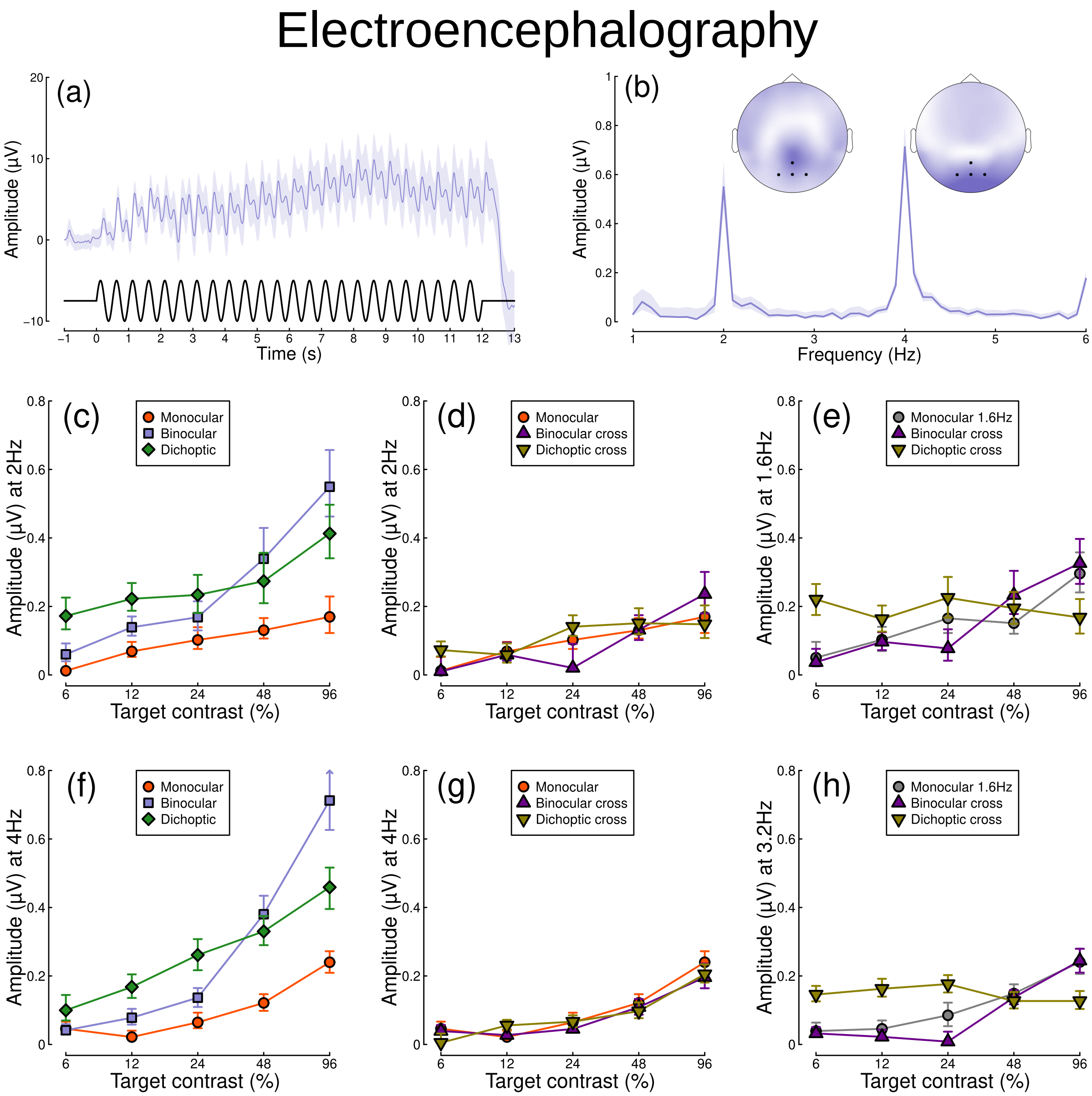

Figure 2: Summary of EEG results for N=30 participants. Panel (a) shows a group average waveform for binocular presentation (low pass filtered at 5Hz), with the driving signal plotted at the foot. Panel (b) shows the average Fourier spectrum, and inset scalp distributions. Black dots on the scalp plots indicate electrodes Oz, POz, O1 and O2. Panels (c,d) show contrast response functions at 2Hz for different conditions. Panel (e) shows contrast response functions at 1.6Hz for three conditions. Panels (f-h) are in the same format but for the second harmonic responses. Shaded regions and error bars indicate bootstrapped standard errors.

Experiment 2

The results from the second experiment are shown in figure 4. In figures 5A to 5C, the curves are showing the results for the monocular and the binocular configurations. In figure 5D, the curves are showing the results for the two harmonics.

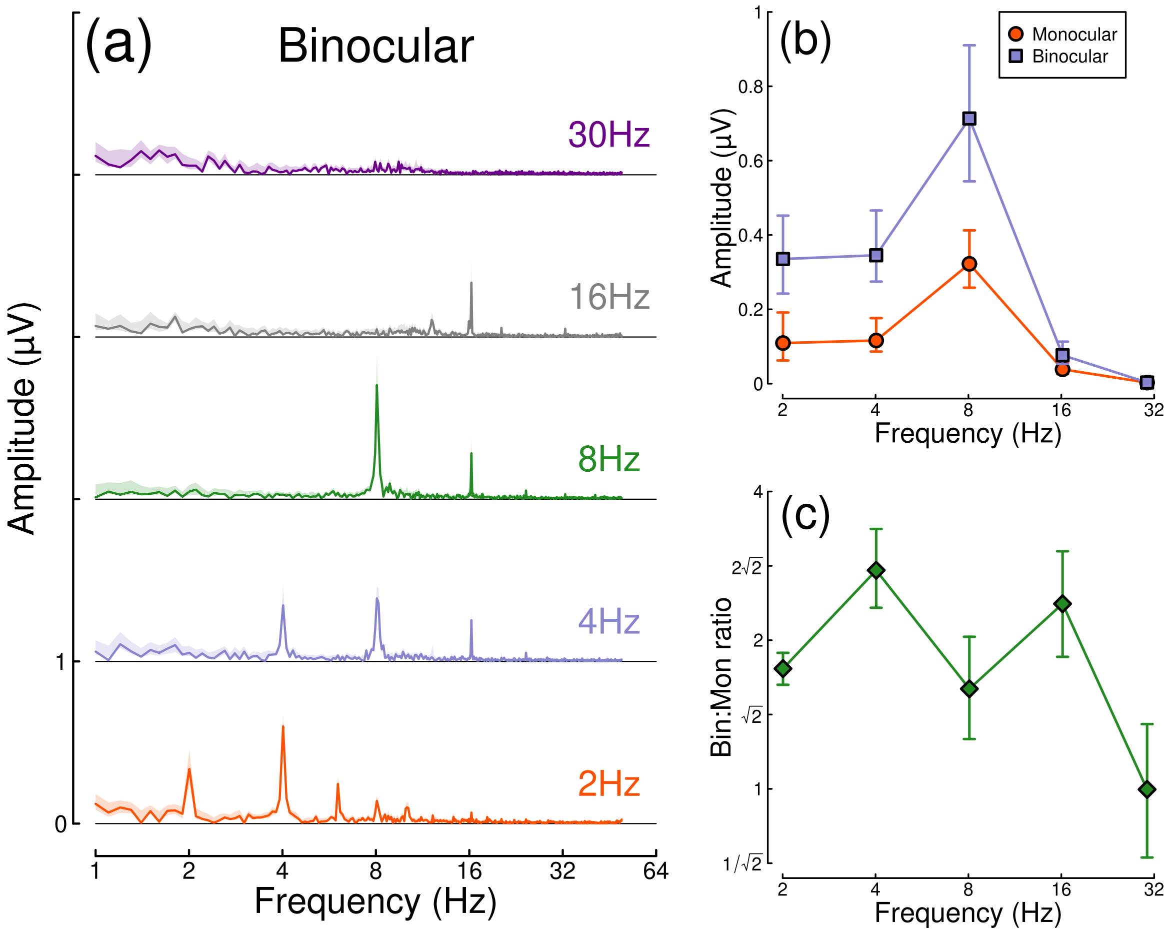

Figure 3: Binocular facilitation at different temporal frequencies. Panel (a) shows Fourier spectra for responses to binocular flicker at 5 different frequencies (offset vertically for clarity). Panel (b) shows the response at each stimulation frequency for monocular (red) and binocular (blue) presentation. Panel (c) shows the ratio of binocular to monocular responses. Error bars and shaded regions indicate bootstrapped standard errors across N=12 participants.

Experiment 3

Computational modelling

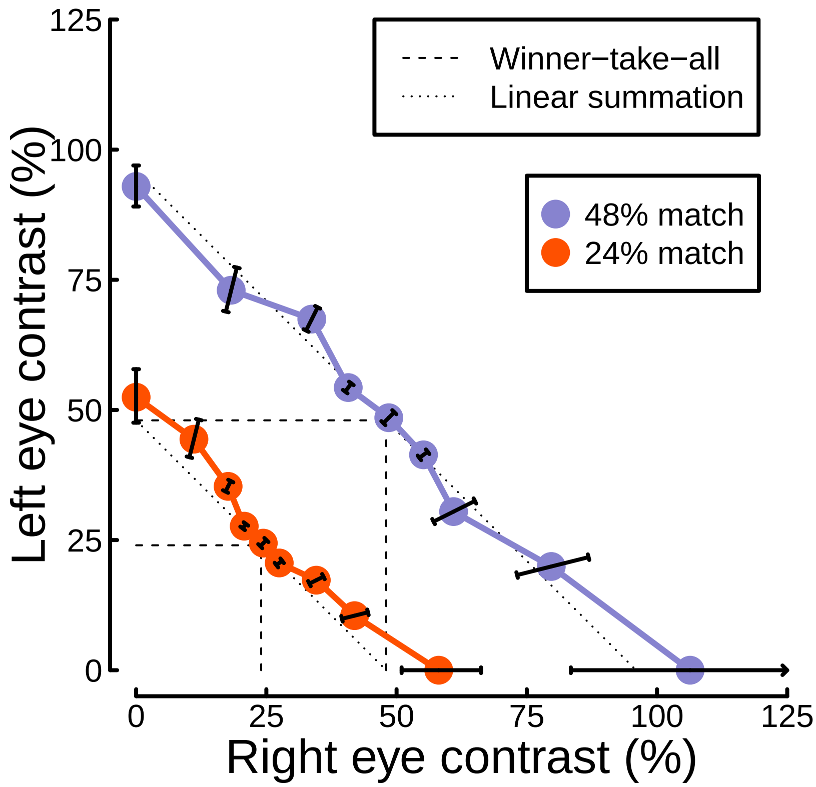

Figure 4: Contrast matching functions. Dotted and dashed lines are predictions of canonical summation models with a linear exponent (dotted) or an infinite exponent (dashed). Error bars indicate the standard error across participants (N=10), and are constrained along radial lines converging at the origin.

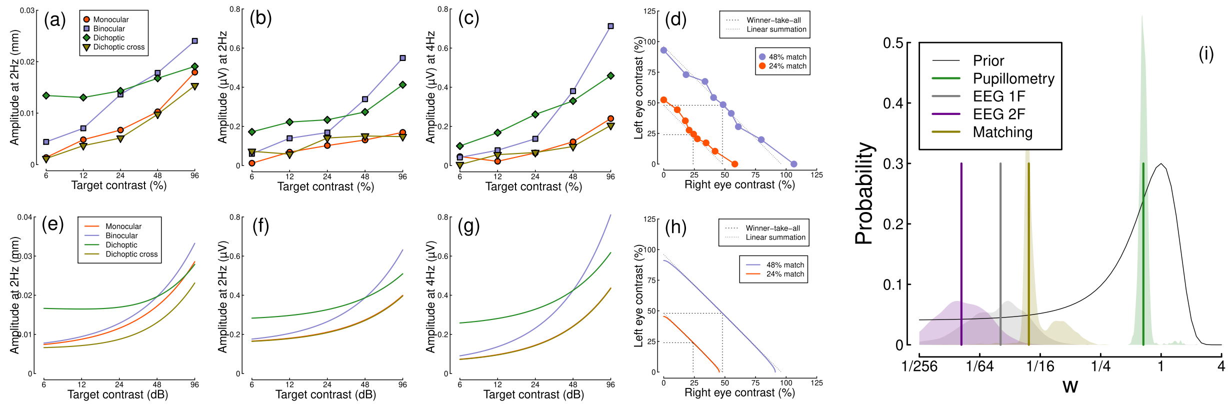

Figure 5: Summary of computational modelling. Panels (a-d) show model behaviour for our four main data set, pupillometry (a), first harmonic EEG responses (b), second harmonic EEG responses (c) and contrast matching (d). Panel (e) shows the posterior probability distributions of the interocular suppression parameter for each of the four model fits. The pupillometry distribution (green) is centred about a substantially higher suppressive weight than for the other data types (note the logarithmic x-axis). The black curve shows the (scaled) prior distribution for the weight parameter.

Table 1: Summary of median parameter values.

Data set	Z	k	w	Rmax
Pupillometry	2.45	0.01	0.67	0.00024
EEG 1F	2.78	0.15	0.03	0.00262
EEG 2F	2.31	0.06	0.01	0.00407
Matching	0.56	7.96	0.05	-

Discussion

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