Contrast gain-control in stereo depth and cyclopean contrast perception

Fang Hou
Laboratory of Brain Processes, Department of Psychology, The Ohio State University, Columbus, OH, USA

Chang-Bing Huang
Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, China

Ju Liang
Vision Research Laboratory, School of Life Science, University of Science and Technology of China, Hefei, Anhui, China

Yifeng Zhou
Vision Research Laboratory, School of Life Science, University of Science and Technology of China, Hefei, Anhui, China

Zhong-Lin Lu
Laboratory of Brain Processes, Department of Psychology, The Ohio State University, Columbus, OH, USA

Although human observers can perceive depth from stereograms with considerable contrast difference between the images presented to the two eyes (Legge & Gu, 1989), how contrast gain control functions in stereo depth perception has not been systematically investigated. Recently, we developed a multipathway contrast gain-control model (MCM) for binocular phase and contrast perception (Huang, Zhou, Lu, & Zhou, 2011; Huang, Zhou, Zhou, & Lu, 2010) based on a contrast gain-control model of binocular phase combination (Ding & Sperling, 2006). To extend the MCM to simultaneously account for stereo depth and cyclopean contrast perception, we manipulated the contrasts (ranging from 0.08 to 0.4) of the dynamic random dot stereograms (RDS) presented to the left and right eyes independently and measured both disparity thresholds for depth perception and perceived contrasts of the cyclopean images. We found that both disparity threshold and perceived contrast depended strongly on the signal contrasts in the two eyes, exhibiting characteristic binocular contrast gain-control properties. The results were well accounted for by an extended MCM model, in which each eye exerts gain control on the other eye’s signal in proportion to its own signal contrast energy and also gain control over the other eye’s gain control; stereo strength is proportional to the product of the signal strengths in the two eyes after contrast gain control, and perceived contrast is computed by combining contrast energy from the two eyes. The new model provided an excellent account of our data ($r^2 = 0.945$), as well as some challenging results in the literature.

Introduction

Depth perception is an amazing achievement in evolution, allowing 3-D perception of the world and judgment of distance. Predators take advantage of the ability to swoop down onto their prey, and tree-living animals exploit it to accurately judge distances when rapidly jumping from branch to branch. One important cue to depth arises because the retinas of the two eyes receive projections of the world from slightly different angles. These differences or horizontal disparities between the views of identical features in the left and right eyes provide disparity cues to depth perception. How images from the two eyes combine to generate cyclopean perception, including perceived depth and appearance of the cyclopean image, has been one of the

In this paper, we investigated effects of image contrast and interocular contrast difference on stereo depth and cyclopean contrast perception by independently manipulating the contrasts of the two monocular images in random dot stereograms (RDS) and measuring both disparity thresholds for depth perception and perceived contrasts of the cyclopean images. The multipathway contrast gain-control model (MCM), previously developed for binocular contrast and/or phase combination (Ding & Sperling, 2006, 2007; Huang, Zhou, Lu, Feng, & Zhou, 2009; Huang, Zhou, Lu, & Zhou, 2011; Huang et al., 2010), was elaborated to simultaneously account for disparity thresholds and perceived contrasts of the cyclopean images. The model also accounted for some challenging data on stereo depth perception in the literature (Cormack et al., 1991; Ding & Levi, 2011; Legge & Gu, 1989).

Effects of image contrast on stereo depth perception

Using narrow-band stimuli, Halpern and Blake (1988) and Legge and Gu (1989) found that the slope of disparity threshold versus (equal) image contrast in the two eyes was around $-0.5$ on a log-log plot, indicating an inverse-square-root dependency of disparity threshold on image contrast. Later, Cormack et al. (1991) found that the log-log slope for high contrast was $-0.33$, comparable with previous findings. At low contrast, however, the slope became closer to $-2$, which indicates an inverse-square dependency of disparity threshold on image contrast. The different slopes in different contrast conditions imply that the relationship between disparity threshold and image contrast is more complex than a simple inverse-square-root or inverse-square law.

Effects of interocular contrast difference on stereo depth perception

Halpern and Blake (1988) also investigated effects of interocular contrast difference on stereo depth perception. They found that disparity threshold increased monotonically when the contrast of the image in one eye was maintained at a fixed high value while the contrast of the image in the other eye decreased successively from that value. For low spatial frequency stimuli, when the contrast of the image in one eye was maintained at a fixed low value while the contrast in the other eye gradually increased from the low value, disparity threshold also increased. Using sine wave gratings, Legge and Gu (1989) found that disparity threshold for stereo depth perception increased as interocular contrast ratio increased. Similar observations have also been reported by Ding and Levi (2011), Schor and Heckmann (1989), and Simons (1984).

In addition, several studies (Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Howarth, 1986) reported that disparity threshold rose more when image contrast was reduced in only one eye than when image contrasts in both eyes were reduced by the same amount. Given that the former condition (image contrast was reduced only in one eye) had more contrast energy than the latter one (image contrast was reduced in both eyes, see Figure 1), Cormack et al. (1991) coined the term “stereo contrast paradox” to refer to the counterintuitive observations. Take the left most two data points in Figure 1 as an example; disparity threshold is greater when the image contrasts in the two eyes were 0.08 and 0.40 than when the contrasts in the two eyes were both at 0.08.

These results, including the stereo contrast paradox, suggest a complex relationship between stereo depth perception and image contrasts in the two eyes.

Existing models on stereo depth perception

Cormack et al. (1991) proposed a cross-correlation model on stereo depth perception. In their model, the strength of the stereo depth signal is proportional to the cross-correlation of the images in the left and right
eyes. The model predicts that disparity threshold is inversely proportional to the product of the contrasts of the images in the two eyes, an inverse-square law when image contrasts are the same in the two eyes. It cannot however explain the disparity threshold function under unequal contrast conditions observed in some experiments (Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckmann, 1989).

In an attempt to explain the observed effects of interocular contrast difference on disparity threshold, Legge and Gu (1989) developed a “peak” model, in which (a) the standard deviation of stimulus location encoding is inversely proportional to the square root of the contrast of the stimulus, (b) the encoded stimulus locations in the two eyes are correlated, and (c) disparity threshold is proportional to the standard deviation of the joint distribution of encoded stimulus peak locations in the two eyes:

\[
D \propto \sqrt{\sigma_L^2 + \sigma_R^2 - 2\rho \sigma_L \sigma_R} = \sqrt{\frac{1}{C_L} + \frac{1}{C_R} - \frac{2\rho}{\sqrt{C_L C_R}}},
\]

where \( D \) is disparity threshold, \( \sigma_L \) and \( \sigma_R \) are the standard deviations of the distributions of the encoded locations of the input images in the left and right eyes with \( \sigma \propto \sqrt{C} \), \( \rho \) is the correlation between the encoded locations in the two eyes, and \( C_L \) and \( C_R \) are image contrasts in the two eyes.

The peak model is consistent with the inverse-square-root relationship between disparity threshold and image contrast and provided a good account for the U-shaped disparity threshold versus contrast ratio (DVR) curves (Legge & Gu, 1989). However, the correlation parameter \( \rho \) in the model is not specified theoretically, and the predicted disparity threshold saturates at large contrast ratios (Kontsevich & Tyler, 1994). Moreover, the correlation parameter might vary with image contrast (Cormack et al., 1991).

Kontsevich and Tyler (1994) proposed an alternative model, which shares the notion of the peak model (Legge & Gu, 1989) that stereo depth is derived from the encoded positions of the images in the two eyes, and the standard deviation of the encoded image location in each eye is proportional to the square root of the contrast of the image. Instead of assuming correlation between the encoded locations of the images in the two eyes (Legge & Gu, 1989), Kontsevich and Tyler (1994) used a weighted binocular summation rule (Schroeder, 1926) in computing disparity threshold:

\[
D \propto \sqrt{\sigma_L^2 + \sigma_R^2} = \sqrt{\frac{1}{w_L C_L} + \frac{1}{w_R C_R}},
\]

where \( w_L = C_L^p/(C_L^p + k C_R^p) \), \( w_R = C_R^p/(C_R^p + k C_L^p) \), and \( p \) is the exponent of the power function.

Although Kontsevich and Tyler’s model is superior to the peak model, there are still some notable issues.

Similar to the peak model, it cannot explain the different slopes of the disparity threshold versus contrast function in low and high contrast conditions. Moreover, the model predicts a disparity threshold even when the contrast of the image in one eye is zero, i.e., only one eye receives an image, and there is obviously no disparity in the stimulus.

Cormack, Stevenson, and Landers (1997) later proposed a hybrid model based on Legge and Gu (1989) and Kontsevich and Tyler (1994). The model incorporates both correlation between the encoded positions in the two eyes and a weighted binocular summation rule:

\[
D \propto \sqrt{\sigma_L^2 + \sigma_R^2 - 2\rho \sigma_L \sigma_R} = \sqrt{\frac{1}{w_L C_L} + \frac{1}{w_R C_R} - \frac{2\rho}{\sqrt{w_L C_L w_R C_R}}},
\]

where \( w_L = C_L^p/(C_L^p + k C_R^p) \), \( w_R = C_R^p/(C_R^p + k C_L^p) \), and \( p \) is the exponent of the power function.

Although the hybrid model provided better fits to their data, Cormack et al. (1997) commented that the hybrid model inherited the shortcomings of its parents: In addition to the frequency dependence implicit in the models (Cormack et al., 1997; Legge & Gu, 1989), the free parameters \( \rho \) and \( k \) could vary non-systematically with spatial frequencies.

**Binocular contrast and phase combination and the multipathway contrast gain-control model (MCM)**

Ding and Sperling (2006) developed a paradigm to measure perceived phase of cyclopean images as a function of the contrasts of the images presented to the two eyes. In this paradigm, two suprathreshold horizontal sine wave gratings of the same spatial frequency but different spatial phases are presented to the left and right eyes of the observer. The perceived phase of the binocularly combined cyclopean image is measured as a function of the contrast ratio between the images in the two eyes. Because the perceived phase of the cyclopean image is determined by the relative amplitudes of the component sine wave gratings at the stage of binocular combination, one can infer the monocular contrast transfer function (how grating contrast is transmitted through each eye) from these measurements. In addition, Ding and Sperling (2006, 2007) proposed a contrast gain-control model of binocular combination in which each eye (a) exerts gain control on the other eye’s signal in proportion to the contrast energy of its own input and (b) additionally exerts gain control on the other eye’s gain control. With a single parameter, the model successfully accounted...
With three free parameters, the model yielded an excellent account of data from all the experimental conditions. The MCM has also been used to successfully characterize deficits in binocular combination in anisometropic amblyopia as a joint mechanism of both attenuation of signals in the amblyopic eye and increased inhibition from the fellow eye to the amblyopic eye (Huang et al., 2011).

In the multipathway contrast gain-control model (MCM) (Figure 2), signals in the two eyes first go through interocular contrast gain control, in which each eye exerts gain control not only on the other eye’s signal (direct inhibition, Path A2 and its counterpart in Figure 2a), but also on the incoming gain-control signal from the other eye (indirect inhibition, Path A3 and its counterpart in Figure 2a), with both effects in proportion to an eye’s own signal contrast energy. After contrast gain control, signal strengths in the two eyes are:

\[
C'_L = C_L \frac{1}{1 + \epsilon_L} , \quad \text{and} \quad C'_R = C_R \frac{1}{1 + \epsilon_R} ,
\]

where

\[
\epsilon_L = \rho C'_L^{\gamma_1}, \quad \text{and} \quad \epsilon_R = \rho C'_R^{\gamma_1},
\]

where \(C_L\) and \(C_R\) are the contrasts of the input images in the left and right eyes, \(\rho\) is the contrast gain-control coefficient, and \(\gamma_1\) is the exponent of the power-law nonlinearity in the gain-control pathway.

The perceived phase and contrast of the cyclopean percept are computed in separate pathways (Huang et al., 2010):

\[
\theta_{\text{perceived}} = 2\tan^{-1}\left(\frac{C_L + \rho C'_L^{1+\gamma_1} - C_R - \rho C'_R^{1+\gamma_1}}{C_L + \rho C'_L^{1+\gamma_1} + C_R + \rho C'_R^{1+\gamma_1}}\tan\left(\frac{\theta}{2}\right)\right) \tag{5a}
\]

\[
C_{\text{perceived}} = \left(C'_L + C'_R\right)^{1/2} = \left(\frac{C_L(1 + \rho C'_L^{\gamma_1})}{1 + \rho C'_L^{\gamma_1}}\right)^{\gamma_2} + \left(\frac{C_R(1 + \rho C'_R^{\gamma_1})}{1 + \rho C'_R^{\gamma_1}}\right)^{\gamma_2} \right)^{1/2} , \tag{5b}
\]

where \(\gamma_2\) is the exponent of the power function in binocular contrast combination.
Elaboration of the MCM to model stereo depth perception

The observed functional relationship between stereo depth perception and image contrast in the literature (Cormack et al., 1991; Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckmann, 1989; Simons, 1984) and results from physiology (Anzai, Ohzawa, & Freeman, 1999a, 1999b; Cumming & DeAngelis, 2001; Grossberg & Howe, 2003; Ohzawa, 1998; Ohzawa & Freeman, 1986a, 1986b) suggest that interocular contrast gain control may play a central role in stereo depth perception. Here, we elaborate the MCM in an attempt to simultaneously model stereo depth perception and binocular contrast combination.

Our formulation of the relationship between disparity threshold and image contrasts in the two eyes is based on the cross-correlation model, which has received support from many psychophysical experiments (Allenmark & Read, 2010, 2011; Banks, Gepshtein, & Landy, 2004; Cormack et al., 1991; Filippini & Banks, 2009; Harris, McKee, & Smallman, 1997; Nienborg, Bridge, Parker, & Cumming, 2004), and has found many successful applications in computer vision (Clerc & Mallat, 2002; Donate, Liu, & Collins, 2011; Heo, Lee, & Lee, 2011; Kanade & Okutomi, 1994). The product rule in the cross-correlation model is consistent with the prevailing disparity energy models of V1 neurons (Anzai et al., 1999a, 1999b; Chen & Qian, 2004; Filippini & Banks, 2009; Ohzawa, 1998; Ohzawa, DeAngelis, & Freeman, 1990, 1996; Qian, 1994, 1997) when the outputs of binocular complex cells with opposite preferred polarities of disparity are compared to extract the polarity of the perceived disparity. In the original cross-correlation model (Cormack et al., 1991), stereo strength is proportional to the product of signal contrasts in the two eyes. Here, we postulate that stereo strength is proportional to the product of the signal strengths in the two eyes after contrast gain control, and disparity threshold is inversely proportional to the power-law nonlinearity in the gain-control pathway, respectively.

Overview

In this study, we independently manipulated the contrasts of the two monocular images of random dot stereograms (RDS) and measured both disparity thresholds for depth perception and perceived contrasts of the cyclopean images. The data provided a strong test of the newly elaborated MCM in its ability to simultaneously account for disparity threshold and perceived contrast in cyclopean perception. In addition, we applied the model to account for some challenging results on stereo depth perception in the literature (Cormack et al., 1991; Ding & Levi, 2011; Legge & Gu, 1989).

Methods

Observers

Three observers, S1 (the first author), S2, and S3, aged 23 to 30 years, participated in the study. All had normal or corrected-to-normal vision and normal stereo acuity (Titmus Fly stereo test, Stereo Optical Co., Inc., Chicago, Illinois). S2 and S3 were naive to the purpose of the study. Written informed consent was obtained before the experiment.

Apparatus

Gamma-corrected stimuli were generated by a PC running Matlab (The Mathworks Corp., Natick, MA) and PsychToolbox subroutines (Brainard, 1997; Pelli, 1997), and displayed on either a Dell 19-in M993s monitor (mean luminance 37.3 cd/m²) for S1 or on a Sony 17-in G220 monitor (mean luminance 22.8 cd/m²) for S2 and S3. Both monitors had 2048 × 1536 pixel resolution and a vertical refresh rate of 60 Hz. The viewing distance was 2.44 m for S1 and 2.22 m for S2 and S3. Different viewing distances were used to match the visual angles of the stimuli on different monitors. A special circuit was used to achieve 14-bit grayscale resolution (Li & Lu, 2012; Li, Lu, Xu, Jin, & Zhou, 2003). Stereoscopes (Geoscope, Standard Mirror Stereoscope) were used to deliver the left and right images of the random dot stereograms to the corresponding eyes. A chin/forehead rest was used to minimize head movement during the experiment.
Stimuli

Dynamic random dot stereograms (RDS) were used in the experiment. Binary random dot patches with a 50% dot density were embedded in a 3.33 degree diameter circular aperture with a black background. Each dot consisted of $10 \times 10$ pixels and subtended 2.5 $\times$ 2.5 minutes of arc of visual angle. The dot patterns in the two eyes were identical except for a relative horizontal shift (disparity) in the target regions in the two eyes. The random dot images in each eye could independently take five possible contrasts: 0.08, 0.16, 0.24, 0.32, and 0.4, leading to a total of 25 possible contrast combinations. The contrast range was carefully chosen to minimize adaptation (Ohzawa & Freeman, 1994). A pilot study showed that the 81.6% correct contrast detection threshold of the dynamic RDS was $< 0.06$ for all observers and eyes. No one
exhibited significantly different detection thresholds in the two eyes.

**Procedure and experimental design**

A two-interval forced choice (2-IFC) task was used to measure disparity threshold. Each trial began with a fixation image (Figure 3a), consisting of a dark fixation dot (diameter of 6.25 min) in the center of a random-dot background (Michelson contrast = 0.2). The vertical and horizontal positions of the two monocular images could be adjusted manually to achieve better convergence in the beginning of each block. After successfully combining the two monocular images into one steady cyclopean image, observers pressed the space bar on the computer keyboard to start the presentation of a 1300-ms dynamic RDS movie. The movie contained two 400-ms stimulus intervals, each consisting of eight frames of independently sampled RDS and delimited by a brief tone in the beginning and a 500-ms interstimulus interval. Dynamic RDS with zero disparity was presented during the 500-ms interstimulus interval. The RDS in one of the randomly chosen intervals contained a horizontal disparity in the lower half of the images in the last six frames, which, if above threshold, could be perceived as being closer to the observer than the upper half of the images; the RDS in the other interval had no horizontal disparity. The two zero disparity frames were introduced in the beginning of each interval to help observers achieve better fusion and to eliminate the difference (if any) between the first and second intervals. Observers were instructed to indicate in which interval they saw stereo images by pressing a key on the computer keyboard. A static RDS with zero disparity was shown in the response period. No feedback was provided. The $\psi$ method (Kontsevich & Tyler, 1999) was used to measure the disparity threshold at 81.6% percentage correct in each contrast combination with 50 trials, for a total of 1,250 trials (25 Combinations $\times$ 50 Trials/Combination) per observer. The slope of the psychometric functions was set to 2.2 in the $\psi$ procedure based on the data from a pilot study. All conditions were randomly intermixed.

Perceived cyclopean contrast was estimated using a contrast matching task and a staircase method. Specifically, each trial began with a fixation image and was followed by six 50-ms dynamic RDS frames that were split into upper and lower halves. The upper half of each RDS frame was a monocular probe that was presented to either the left or right eye, with a blank image with background luminance in the other eye. The lower half of each RDS frame contained images in both eyes. The random dot image in the lower half of each eye was independently assigned one of five possible contrasts: 0.08, 0.16, 0.24, 0.32, and 0.4. The disparity of the random dot stereogram in the lower half was either crossed or uncrossed and set at around twice of the individual’s largest disparity threshold measured using stereograms with a 0.08 contrast in both eyes. Observers were instructed to first report whether the lower half of the RDS was in front of (crossed) or behind (uncrossed) the fixation dot, and then which part, the upper or lower half of the image, had a higher contrast. The fixation point, present in the middle of the screen throughout the entire trial, served as the reference for depth discrimination.

The contrast of the probe was controlled by a truncated staircase that converged to 50%. Only trials with correct depth judgment were tracked by the staircase. The staircases for different contrast combinations were interleaved. There were 50 Trials $\times$ 25 Contrast Combinations $\times$ 2 Eye Origin of Probe $\times$ 2 Depths (crossed and uncrossed), with 5,000 trials in total for each observer. The perceived contrast of cyclopean image could thus be expressed by the matched probe contrast in the left or right eyes, which was calculated as the average of the probe contrasts in the upper half, taken at a minimum of 10 reversal points in the staircase.

**Data analysis**

Within-observer analysis of variance (ANOVA) was used to test whether matched probe contrast depended on the contrasts of the images in the two eyes, eye origin of the probe, depth polarity (crossed and uncrossed), and their interactions, and whether disparity threshold depended on contrasts in the two eyes.

All the model-fitting programs were implemented in Matlab (MathWorks). The summed squares of the differences between model predictions and observed values, $SSE = \sum(y_i - \hat{y}_i)^2$, where $y_i$ and $\hat{y}_i$ represented the observed and predicted values, respectively, and the sum of total squared errors, $SST = \sum(y_i - \bar{y})^2$, where $\bar{y}$ is the mean of $y_i$, were computed separately for disparity thresholds and perceived contrasts in term of matched probe contrasts in the left and right eyes. We define $r^2$ as:

$$r^2 = \frac{SSE}{SST} = \frac{\sum(y_i - \hat{y}_i)^2}{\sum(y_i - \bar{y})^2}.$$  

(7)

The average $r^2$, ($r^2_d + r^2_{C_L} + r^2_{C_R}$)/3, where $r^2_d$, $r^2_{C_L}$, and $r^2_{C_R}$ are $r^2$’s for disparity threshold, matched probe contrasts in the left and right eyes, was used as the cost function in a modified least-squares procedure in fitting
the model to the data. The goodness of fit of the MCM was also evaluated by the average $r^2$.

An $F$ test was used to statistically compare the performance of nested models:

$$F(df_1, df_2) = \frac{(r^2_{\text{full}} - r^2_{\text{reduced}})/df_1}{(1 - r^2_{\text{full}})/df_2},$$

where $df_1 = k_{\text{full}} - k_{\text{reduced}}$, $df_2 = N - k_{\text{full}}$; $k_{\text{full}}$ and $k_{\text{reduced}}$ are the numbers of parameters of the full and reduced models, respectively, and $N$ is the number of data points.

**Results**

**Effects of image contrasts on perceived cyclopean contrast**

Matched probe contrasts of the cyclopean images for the three observers are plotted as bivariate functions of image contrasts in the left and right eyes in Figure 4. An analysis of variance (ANOVA) revealed that matched probe contrast of cyclopean images varied significantly with test image contrasts in both eyes, $F(4, 8) = 506$, $p = 1.20 \times 10^{-9}$, for the probe in the nondominant eye; $F(4, 8) = 140$, $p = 1.95 \times 10^{-7}$, for the probe in the dominant eye. There was also a significant interaction between the test contrasts in the two eyes, $F(16, 32) = 56.1$, $p = 2.23 \times 10^{-308}$. There was no significant effect of depth polarity, $F(1, 2) = 4.22$, $p = 0.176$. The matched contrasts were averaged across the uncrossed and crossed depth conditions in subsequent analyses. As we noted in Figure 4, the matched probe contrasts in the left eye were systematically deviated from those in the right eye for all observers, there was a significant effect of the eye origin of the probe, $F(1, 2) = 44.0$, $p = 0.022$.

Because the same stimuli were used in the lower half of the stereograms to construct the cyclopean images, different resulting matches obtained with probes in the two different eyes suggest that image contrasts in the two eyes were not represented equally. To characterize the difference of the matched probe contrasts for the cyclopean images between two eyes, a straight line through the origin:

$$C_{\text{matched, probe in } R} = bC_{\text{matched, probe in } L},$$

where $b$ is the slope, was fitted to the matched probe...
Effects of contrast on disparity threshold

The observed disparity thresholds are plotted as functions of image contrasts in the left and right eyes for each observer in Figure 5. Generally, when image contrast in one eye was low (e.g., 0.08), measured disparity threshold dropped rapidly as image contrast in the other eye increased; when image contrast in one eye was high (e.g., 0.4), disparity threshold dropped slowly as image contrast in the other eye increased. Disparity thresholds depended significantly on image contrasts in both the dominant, $F(4, 8) = 46.5, p = 1.40 \times 10^{-5}$, and nondominant, $F(4, 8) = 29.4, p = 7.81 \times 10^{-5}$, eyes. The interaction between image contrasts in the two eyes was marginally significant, $F(16, 32) = 1.87, p = 0.064$.

To explore the relationship between disparity threshold and image contrast, we graphed disparity threshold as a function of the product of the contrasts in the two eyes on a log-log plot (Figure 6). The data points with image contrast in the left eye equal to, greater than, or less than that in the right eye are plotted with different symbols. Two straight lines of slopes $-1$ and $-0.25$, which represent the inverse-square and inverse-square-root dependency on contrast, are overlaid on the graph.

Generally, disparity threshold decreased as contrast product increased. When the contrasts in the two eyes are equal (black squares), the slope of the threshold versus contrast product curve is neither $-1$ nor $-0.25$ for all observers, suggesting that disparity threshold cannot simply be described by an inverse-square or inverse-square-root function on contrast. Taking all data points (with equal and unequal contrasts in the two eyes) into account, the overall slope of the threshold versus contrast product function was $-0.725$, $-0.509$, and $-0.594$ for S1, S2, and S3, respectively.

In addition, for S1, the imbalance between the left and right eyes revealed in the binocular contrast combination task was also found in the disparity threshold data: The threshold was higher when the contrast in the left eye was greater than that in the opposite direction.

Earlier studies (Cormack et al., 1991; Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckmann, 1989) have found that disparity threshold depended on image contrasts in both eyes as well as interocular contrast difference between the two eyes. To illustrate the effect of unequal image contrasts in the two eyes, we replotted the observed disparity threshold as...
functions of interocular contrast ratios in Figure 7 using the format developed in Legge and Gu (1989). The disparity threshold versus contrast ratio functions (DVR) are U-shaped. Increasing contrast ratio increased disparity threshold. The results are consistent with Legge and Gu (1989).

Several studies (Cormack et al., 1997; Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckmann, 1989) have found a phenomenon called stereo contrast paradox using narrow band stimuli, in which disparity threshold rose more when image contrast in only one eye was reduced than when image contrasts in both eyes were reduced by the same amount. In Figure 8, we plotted the observed disparity thresholds as a function of image contrast in one eye while keeping image contrast in the other eye fixed at 0.4, along with the disparity thresholds when image contrasts were reduced in both eyes by the same amount. Inconsistent with those studies in the literature, we found that disparity threshold rose more rapidly when image contrasts were reduced in both eyes than when contrast was reduced in only one eye. In other words, we did not observe the stereo contrast paradox. The absence of stereo contrast paradox with RDS has also been reported by Cormack et al. (1997) who used RDS and high spatial frequency narrow-band stimuli. We discuss potential explanations in the Discussion.

Figure 6. Disparity threshold versus product of image contrasts in the two eyes. Squares: image contrasts in the left and right eyes were equal. Circles: image contrast in the left eye was greater than that in the right eye. Triangle: image contrast in the left eye was less than that in the right eye. Dash lines represent the predictions of an inverse-square and inverse-square-root dependency. Solid line: linear regression of all data points. Error bars represented ±1 SD.

Figure 7. Disparity threshold as a function of image contrast ratio between the left and right eyes and the right and left eyes for observers S1, S2, and S3. The higher contrast was fixed at 0.08 (red circle), 0.16 (green square), 0.24 (blue asterisk), 0.32 (cyan cross), or 0.4 (purple triangle). Error bars represented ±1 SD.
Figure 8. Black circles: disparity threshold as a function of (equal) image contrasts in the two eyes. Red triangles: disparity threshold as a function of image contrast in the left eye while image contrast in the right eye was kept at 0.4. Blue triangles: disparity threshold as a function of image contrast in the right eye while image contrast in the left eye was kept at 0.4. Error bars represent ±1 SD.

Model fit

Because of the observed asymmetry of the two eyes in our data, we adopted an elaborated MCM developed by Huang et al. (2011) in the context of amblyopic vision that modeled imbalanced processing of information in the two eyes with three mechanisms: (a) attenuation of signal contrast in the nondominant eye (η), (b) stronger direct inhibition from the dominant eye (α), and (c) stronger indirect inhibition (β) from the dominant eye to the gain control signal coming from the nondominant eye. For simplicity, here we assume the left eye is the dominant eye in these equations. In cases where the right eye dominates, we simply reverse the symbols.

In the elaborated model, after contrast gain control, signal strengths in the two eyes are:

\[ C'_L = C_L \frac{1}{1 + \frac{\varepsilon_L}{1 + \beta/\alpha}}, \quad C'_R = C_R \frac{1}{1 + \frac{\varepsilon_R}{1 + \alpha/\beta}}, \]

where

\[ \varepsilon_L = \rho C_L^{\gamma_1}, \quad \varepsilon_R = \rho (\eta C_R)^{\gamma_1}, \]

(10)

\( C_L \) and \( C_R \) are the contrasts in the left and right eyes, \( \rho \) is the contrast gain-control efficiency, \( \eta \) is used to model contrast attenuation in right eye, \( \alpha, \beta \) are used to model the stronger inhibition to the right eye from the left eye, and \( \gamma_1 \) is the transducer nonlinearity in the gain-control pathway.

The perceived contrast of the cyclopean image becomes (Huang et al., 2011):

\[
C_{\text{perceived}} = \left( \frac{C_L (1 + \beta \rho C_L^{\gamma_1})}{1 + \beta \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2} + \left( \frac{\eta C_R (1 + \rho (\eta C_R)^{\gamma_1})}{1 + \alpha \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2},
\]

(11)

where \( \gamma_2 \) is the transducer nonlinearity for the power summation in binocular contrast combination. Thus, when the probe is presented to different eyes, we have:

\[
C_{\text{matched, probe in } L} = \left( \frac{C_L (1 + \beta \rho C_L^{\gamma_1})}{1 + \beta \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2} + \left( \frac{\eta C_R (1 + \rho (\eta C_R)^{\gamma_1})}{1 + \alpha \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2},
\]

(12a)

and

\[
C_{\text{matched, probe in } R} = \frac{1}{\eta} \left( \frac{C_L (1 + \beta \rho C_L^{\gamma_1})}{1 + \beta \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2} + \left( \frac{\eta C_R (1 + \rho (\eta C_R)^{\gamma_1})}{1 + \alpha \rho C_L^{\gamma_1} + \rho (\eta C_R)^{\gamma_1}} \right)^{1/\gamma_2}.
\]

(12b)
For all observers, the reduced Model 2 and full compared by the nested model test.

c conducive eye dominance in our data. To explore whether the attenuation mechanism alone is enough to account for the observed imbalance between the two eyes in our data. The elaborated MCM with the attenuation mechanism was statistically comparable to the full model with all three mechanisms for Observers S2 and S3, accounting for 91.9% and 93.8% of the variance in the data. On the other hand, the full model with three mechanisms is superior to its reduced versions, \( F(2, 68) = 6.80, p = 0.002 \), and accounts for 98.0% of the data for S1, suggesting stronger inhibition from the dominant eye to the nondominant eye in addition to monocular attenuation. The predictions of the best fitting models are plotted in Figure 9.

**Fitting the MCM to some challenging data in the literature**

Cormack et al. (1991) measured disparity threshold of RDS as a function of image contrasts in the two eyes. The data were extracted from their paper and replotted in Figure 10. In their study, the RDS were presented with image contrasts at multiples of the detection threshold, so an MCM with four parameters \((k, \rho, \gamma_1, \text{and contrast threshold } \tau)\) was fitted to the data. The MCM accounted for 95.9% and 90.4% of the variance of the data for observers LKC and CMS, respectively (for detail of best fitting parameters, see Table 21). Generally speaking, the MCM provided better fits than the inverse-square or inverse-square-root functions, although there is some misfit in the high contrast conditions (see Discussion).

Legge and Gu (1989) measured disparity threshold of sinusoidal gratings as a function of interocular contrast ratio. We extract the data from their paper and replotted them in Figure 11. There were two sets of data measured at 0.5 cycles/° and 2.5 cycles/°. The higher contrast in one eye was fixed at either 0.125 or 0.25. The full MCM with attenuation and inhibition mechanisms was used because of the evident imbalance of the two eyes in the data (see figure 6 in Legge & Gu, 1989). To further constrain the MCM, the same set of parameters \((k, \rho, \gamma_1, \eta, \alpha, \text{and } \beta)\) were used to account for all the data in one spatial frequency condition for each observer. The best fitting results are plotted in Figure 11. For DR, \( r^2 = 0.929 \) and 0.970 in the 0.5 cycles/° and 2.5 cycles/° conditions, respectively. For KD, \( r^2 = 0.974 \) and 0.965 in the 0.5 cycles/° and 2.5 cycles/° conditions, respectively (Table 2).

Ding and Levi (2011) measured phase disparity threshold for amblyopic observers using Legge & Gu's

### Table 1. Parameters of best fitting MCM models for all observers and comparisons between them.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Model</th>
<th>( k )</th>
<th>( \rho )</th>
<th>( \gamma_1 )</th>
<th>( \gamma_2 )</th>
<th>( \eta )</th>
<th>( \alpha )</th>
<th>( \beta )</th>
<th>( r^2 )</th>
<th>Comparison</th>
<th>( F )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>Reduced1</td>
<td>0.013</td>
<td>36.8</td>
<td>1.56</td>
<td>0.828</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.942</td>
<td>Reduced1, Reduced2</td>
<td>99.2</td>
<td>4.77 × 10^{-15}</td>
</tr>
<tr>
<td></td>
<td>Reduced2</td>
<td>0.012</td>
<td>40.3</td>
<td>1.57</td>
<td>0.826</td>
<td>0.903</td>
<td>-</td>
<td>-</td>
<td>0.976</td>
<td>Reduced1, Full</td>
<td>43.1</td>
<td>9.99 × 10^{-16}</td>
</tr>
<tr>
<td></td>
<td>Full</td>
<td>0.022</td>
<td>28.0</td>
<td>2.23</td>
<td>1.28</td>
<td>0.916</td>
<td>1</td>
<td>4.47</td>
<td>0.980</td>
<td>Reduced2, Full</td>
<td>6.80</td>
<td>0.002</td>
</tr>
<tr>
<td>S2</td>
<td>Reduced1</td>
<td>0.017</td>
<td>6.22</td>
<td>1.39</td>
<td>0.902</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.887</td>
<td>Reduced1, Reduced2</td>
<td>27.7</td>
<td>1.48 × 10^{-6}</td>
</tr>
<tr>
<td></td>
<td>Reduced2</td>
<td>0.016</td>
<td>6.71</td>
<td>1.40</td>
<td>0.909</td>
<td>0.888</td>
<td>-</td>
<td>-</td>
<td>0.919</td>
<td>Reduced1, Full</td>
<td>9.35</td>
<td>3 × 10^{-5}</td>
</tr>
<tr>
<td></td>
<td>Full</td>
<td>0.018</td>
<td>7.22</td>
<td>1.63</td>
<td>1.02</td>
<td>0.891</td>
<td>1</td>
<td>1.72</td>
<td>0.920</td>
<td>Reduced2, Full</td>
<td>0.425</td>
<td>0.656</td>
</tr>
<tr>
<td>S3</td>
<td>Reduced1</td>
<td>0.017</td>
<td>6.55</td>
<td>1.25</td>
<td>0.910</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.931</td>
<td>Reduced1, Reduced2</td>
<td>7.90</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Reduced2</td>
<td>0.016</td>
<td>6.51</td>
<td>1.25</td>
<td>0.912</td>
<td>0.950</td>
<td>-</td>
<td>-</td>
<td>0.938</td>
<td>Reduced1, Full</td>
<td>3.40</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>Full</td>
<td>0.016</td>
<td>6.45</td>
<td>1.22</td>
<td>0.880</td>
<td>0.950</td>
<td>1.14</td>
<td>1</td>
<td>0.940</td>
<td>Reduced2, Full</td>
<td>1.13</td>
<td>0.328</td>
</tr>
</tbody>
</table>
procedure (1989). The data were extracted from their paper for observer GD, consisting of three conditions with the higher contrast in one eye fixed at 0.24, 0.48, and 0.96. The full MCM including attenuation and inhibition was adopted for the amblyopic observer, with a total of six parameters. The same set of parameters was used to account for the three data sets for GD. The MCM provided very good accounts of the data ($r^2 = 0.859$, Figure 12, Table 2).

**Discussion**

In this study, we measured disparity threshold and perceived contrast of dynamic RDS with different image contrast combinations in the two eyes. We found that both disparity threshold and cyclopean contrast depend strongly on test image contrasts in the two eyes, exhibiting characteristic binocular contrast-gain control properties, consistent with previous findings with narrow-band stimuli (Halpern & Blake, 1988; Legge &
We extended the MCM (Huang et al., 2011; Huang et al., 2010) to account for the full dataset. The new MCM adopted the idea that cyclopean perception of contrast and depth shared the same front-end binocular contrast gain control, in which each eye exerts gain control on the other eye’s signal in proportion to its own signal contrast energy, and also gain controls over the other eye’s incoming gain control. After interocular contrast gain control, the outputs are processed by different pathways to compute perceived phase, contrast, and depth. The extended MCM provided very good accounts for the observed disparity thresholds and cyclopean contrasts with the same set of parameters.

Independent pathway for contrast perception

The MCM was originally proposed to model perceived phase and contrast during binocular combination (Huang et al., 2010) with separated pathways for contrast and phase perception. Here, we found that perceived cyclopean contrast did not depend on the disparity polarity of the RDS stimuli. An independent pathway for contrast perception is consistent with the literature. For example, the response of complex cell in V1 is phase invariant (Carandini et al., 2005; Hyvarinen, Hurri, & Hoyer, 2009). The prevailing energy model of complex cells, which combines inputs from the quadrature pairs of its subunits to produce feature-selective but phase-invariant response is very successful in accounting for edge/line detection, motion detection, and disparity extraction (Adelson & Bergen, 1985; Emerson, Bergen, & Adelson, 1992; Morrone & Burr, 1988; Ohzawa, 1998; Ohzawa et al., 1990). Also, contrast constancy, first introduced by Georgeson and Sullivan (1975), is an important function of visual system. Contrast constancy has been found in stimuli with coherent and incoherent phase spectra (Brady & Field, 1995), and is independent of size, spatial frequency, bandwidth of the stimuli (Cannon & Fullenkamp, 1988; Georgeson & Sullivan, 1975; Tiippana & Nasanen, 1999). In our experiment, only depth polarity was manipulated. Future studies with a wide range of disparities are necessary to examine whether perceived contrast is independent of the magnitude of stereo depth.

Stereo contrast paradox

Consistent with the literature, we found that the relationship between disparity threshold and image contrast (when contrasts are equal in two eyes) couldn’t be simply described by an inverse-square or inverse-square-root function (Cormack et al., 1991), and the disparity threshold versus contrast ratio function was U-shaped (Ding & Levi, 2011; Legge & Gu, 1989). There are however some discrepancies.

![Figure 10. MCM fits to the disparity threshold data reported in Cormack et al. (1991) (replotted with permission).](image)

Table 2. Parameters of best fitting MCM models for data in the literature.

<table>
<thead>
<tr>
<th>Data</th>
<th>Observer</th>
<th>k</th>
<th>$\rho$</th>
<th>$\gamma_1$</th>
<th>$\tau$</th>
<th>$\eta$</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cormack et al. (1991)</td>
<td>LKC</td>
<td>0.026</td>
<td>$5.66 \times 10^4$</td>
<td>4.32</td>
<td>0.012</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.959</td>
</tr>
<tr>
<td></td>
<td>CMS</td>
<td>0.011</td>
<td>426</td>
<td>2.13</td>
<td>0.012</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.904</td>
</tr>
<tr>
<td>Legge and Gu (1989)</td>
<td>DR, SF = 0.5</td>
<td>$8.00 \times 10^{-4}$</td>
<td>$4.80 \times 10^6$</td>
<td>3.85</td>
<td>-</td>
<td>1.65</td>
<td>1</td>
<td>0.929</td>
<td></td>
</tr>
<tr>
<td></td>
<td>DR, SF = 2.5</td>
<td>$4.00 \times 10^{-4}$</td>
<td>$1.22 \times 10^6$</td>
<td>3.20</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>1.05</td>
<td>0.970</td>
</tr>
<tr>
<td></td>
<td>KD, SF = 0.5</td>
<td>0.020</td>
<td>364</td>
<td>2.11</td>
<td>-</td>
<td>1</td>
<td>1.24</td>
<td>1</td>
<td>0.974</td>
</tr>
<tr>
<td></td>
<td>KD, SF = 2.5</td>
<td>0.002</td>
<td>$3.57 \times 10^6$</td>
<td>2.29</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>2.24</td>
<td>0.965</td>
</tr>
<tr>
<td>Ding and Levi (2011)</td>
<td>GD</td>
<td>2.13</td>
<td>16.1</td>
<td>1.56</td>
<td>-</td>
<td>1</td>
<td>1.24</td>
<td>1</td>
<td>0.859</td>
</tr>
</tbody>
</table>
Some previous studies showed that, with narrow-band stimuli, disparity threshold increased more when image contrast in one eye was reduced than when image contrasts in both eyes were reduced by the same amount (Cormack et al., 1997; Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckmann, 1989), a phenomenon referred to as stereo contrast paradox (Cormack et al., 1997). However, using RDS in this study, we did not observe stereo contrast paradox. Cormack et al. (1997) also did not find stereo contrast paradox with RDS and high spatial frequency narrow-band stimuli. They concluded that the paradox is restricted to low spatial frequencies and suggested the absence of the paradox was due to different processing of low- and high-spatial frequency information by the visual system (Cormack et al., 1997; Stevenson & Cormack, 2000).

In the MCM with balanced processing of information from the two eyes (Equation 6), disparity threshold is $D_{eq} = \frac{k(1 + \rho C^{\gamma_1})}{\sqrt{C^{\gamma_1}(1 + \rho C^{\gamma_1})}}$ when image contrasts in the two eyes are equal; disparity threshold is $D_{ineq} = \frac{k(1 + \rho C^{\gamma_1} + \rho C_0^{\gamma_1})^2}{C_0(1 + \rho C_0^{\gamma_1})} - \frac{(1 + 2\rho C^{\gamma_1})^2}{C(1 + \rho C^{\gamma_1})}$ when image contrast is $C$ in one eye and $C_0$ in the other eye. Stereo contrast paradox results when $D_{ineq} - D_{eq} > 0$, and therefore:

$$\frac{(1 + \rho C^{\gamma_1} + \rho C_0^{\gamma_1})^2}{C_0(1 + \rho C_0^{\gamma_1})} - \frac{(1 + 2\rho C^{\gamma_1})^2}{C(1 + \rho C^{\gamma_1})} > 0$$

In other words, in a given condition $(C, C)$ and $(C, C_0)$, whether stereo contrast paradox occurs is determined by two parameters, $\rho$ and $\gamma_1$, in the MCM.

In Figure 13, we plot the magnitude of stereo contrast paradox ($D_{ineq} - D_{eq}$) as a function of $\rho$ and $\gamma_1$ when image contrasts in the two eyes are $(0.08, 0.4)$ and $(0.08, 0.4)$. The area with positive threshold difference indicates parameter combinations that pro-
duce stereo contrast paradox: \( \rho > 49 \) and \( 1.8 < \gamma_1 < 6 \). One possible reason that some studies found stereo contrast paradox and some did not is that different experimental conditions, e.g., spatial frequency content and duration of the stereograms, may have invoked different \( \rho \) and \( \gamma_1 \).

In the MCM with imbalanced processing of information from the two eyes (Equation 13), whether stereo contrast paradox occurs is determined by \( \rho \) and \( \gamma_1 \) as well as monocular attenuation (\( \eta \)) and interocular inhibition (\( \alpha \) and \( \beta \)). Stereo contrast paradox could occur because of imbalanced processing even in combinations of \( \rho \) and \( \gamma_1 \) for which stereo contrast paradox would not occur if the two eyes were balanced. In Figure 14, we plot the magnitude of stereo contrast paradox as a function of \( \eta \) and \( \alpha \) (\( = \beta \)) between conditions when image contrasts in the two eyes are both 0.08 and when image contrast is 0.08 in the nondominant eye and 0.4 in the dominant eye for an observer with \( \rho = 76.5 \) and \( \gamma_1 = 1.11 \).

Figure 14. Predicted threshold difference \( (D_{\text{ineq}} - D_{\text{eq}}) \) as a function of \( \eta \) and \( \alpha \) (\( = \beta \)) between conditions when image contrasts in the two eyes are both 0.08 and when image contrast is 0.08 in the nondominant eye and 0.4 in the dominant eye for an observer with \( \rho = 76.5 \) and \( \gamma_1 = 1.11 \).

The MCM

The MCM provided an excellent account of the data from three normal observers. It also provided good fits to some very challenging data in the literature (Cormack et al., 1991; Ding & Levi, 2011; Legge & Gu, 1989). It’s noteworthy that there are some slight but systematic misfits when image contrast was 15 times or more above threshold (Figure 11). When stimulus contrast increases, the contrast response function of neurons in V1 exhibits compression and saturation (Albrecht & Hamilton, 1982). In the high contrast range, the gain parameter \( \rho \) in the MCM may start to vary as a function of contrast (Albrecht & Geisler, 1991; Heeger, 1992; Ohzawa & Freeman, 1994), before the binocular interaction stage. That is why we carefully chose the range of contrast (0.08 \( \sim \) 0.4) in the current study. The MCM may need a more sophisticated contrast response function in high contrast conditions.

There is evidence that, in addition to decreased monocular visual acuity and contrast sensitivity (Ciuffreda, Levi, & Selenow, 1991; McKee, Levi, & Movshon, 2003), people with amblyopia also exhibit abnormal stereoaucuity (Ciuffreda et al., 1991; Goodwin & Romano, 1985; Walraven & Janzen, 1993). However, whether the abnormal stereopsis of amblyopia is due to decreased contrast sensitivity or interocular inhibition or both is an interesting question. Research on stereo depth perception in amblyopia based on the MCM may shed important light on the mechanisms of deficits in stereo vision in that population.

Taken together, the extended MCM has successfully accounted for the empirical data on stereo depth and cyclopaean contrast perception in a wide range of contrast conditions from the current and previous studies. The hypothesis of multiple pathways with shared front-end binocular interaction for phase, contrast, and stereopsis is compatible with our knowledge of the visual system. Investigation on other phenomena in binocular vision, i.e., binocular rivalry (Blake, 2001; Blake & Fox, 1974; Lee, Blake, & Heeger, 2007; Logothetis, Leopold, & Sheinberg, 1996) and interocular masking (Baker & Graf, 2009) could provide further tests for the MCM.

Keywords: depth perception, binocular vision, contrast, gain-control, disparity
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Corresponding author: Zhong-Lin Lu.
Email: lu.535@osu.edu.
Address: Laboratory of Brain Processes, Department of Psychology, The Ohio State University, Columbus, OH.

Footnote

1Large $q$s are not a problem—in the MCM, a large $q$ means that the contribution of contrast energy is much greater than one; in that case, the $q$ would drop out of the equations.

References


Cormack, L. K., Stevenson, S. B., & Schor, C. M.


