Binocular contrast vision at and above threshold

Tim S. Meese   School of Life and Health Sciences, Aston University, Birmingham, UK

Mark A. Georgeson   School of Life and Health Sciences, Aston University, Birmingham, UK

Daniel H. Baker   School of Life and Health Sciences, Aston University, Birmingham, UK

A fundamental problem for any visual system with binocular overlap is the combination of information from the two eyes. Electrophysiology shows that binocular integration of luminance contrast occurs early in visual cortex, but a specific systems architecture has not been established for human vision. Here, we address this by performing binocular summation and monocular, binocular, and dichoptic masking experiments for horizontal 1 cycle per degree test and masking gratings. These data reject three previously published proposals, each of which predict too little binocular summation and insufficient dichoptic facilitation. However, a simple development of one of the rejected models (the twin summation model) and a completely new model (the two-stage model) provide very good fits to the data. Two features common to both models are gently accelerating (almost linear) contrast transduction prior to binocular summation and suppressive ocular interactions that contribute to contrast gain control. With all model parameters fixed, both models correctly predict (1) systematic variation in psychometric slopes, (2) dichoptic contrast matching, and (3) high levels of binocular summation for various levels of binocular pedestal contrast. A review of evidence from elsewhere leads us to favor the two-stage model.

Keywords: model, human vision, psychophysics, binocular interactions, suppression, summation, gain control, masking

Introduction

A fundamental encoding strategy in biological vision is the representation of the retinal image in terms of local luminance contrast. Over the last 40 years, this process has received extensive psychophysical examination using sine-wave gratings (or similar) and a variety of detection, discrimination, and masking paradigms. The process has come to be understood in terms of parallel spatial filters, each with a single stage of contrast gain control. A given mechanism (or filter kernel) has an accelerating response nonlinearity (typically a square law or greater) and is suppressed by a pool of other mechanisms viewing either the same or similar retinal locations (Albrecht & Geisler, 1991; Foley, 1994; Heeger, 1992; Holmes & Meese 2004; Meese & Hess, 2004; Ross & Speed, 1991; Tolhurst & Heeger, 1997). Most of the psychophysical work has used binocular stimulation, and thus, the properties of monocular pathways and the manner of their combination and interaction have remained obscure. One exception to this is the pioneering work of Legge. He assembled a set of psychophysical tests and an outline of a binocular vision model (see Results section) that have become established benchmarks (Foley & Legge, 1981; Legge, 1979, 1984a, 1984b). However, the model was not fully developed, and the sparseness of the data sets makes their rigorous quantitative examination difficult. It is also unclear how con-

temporary views of contrast gain control might affect Legge's scheme, although preliminary suggestions have been made (Ding & Sperling, 2006; Maehara & Goryo, 2005; Meese & Hess, 2004).

Binocular summation at threshold

Aside from Legge's work, normal binocular interactions above threshold have received little attention by signal detection theorists. However, there have been many experimental studies at contrast detection threshold (e.g., Arditi, Anderson, & Movshon, 1981; Blake & Levinson, 1977; Blake & Rush, 1980; Campbell & Green, 1965; Green & Blake, 1981; Legge, 1984a; Lema & Blake, 1977; Rose, 1978, 1980; Simmons, 2005; Snowden & Hammett, 1998; Valberg & Fosse, 2002; see Blake & Fox, 1973, and Blake, Sloane, & Fox, 1981, for extensive reviews of early work). Two widely cited studies reported a binocular summation ratio (the ratio of monocular to binocular contrast detection thresholds) around $\sqrt{2}$ (Campbell & Green, 1965; Legge, 1984a). In fact, greater levels of summation were acknowledged in this early work (Legge, 1984a) and have been found several times since (e.g., Meese & Hess, 2004, 2005; Rose, 1980; Simmons, 2005), but little has been done to emphasize departures from $\sqrt{2}$. Perhaps one factor in the persistence of the $\sqrt{2}$ figure (Blake et al., 1981; Smith,

Chino, Ni, & Cheng, 1997; Strasburger, 2001) is its theoretical convenience. Campbell and Green proposed a model where the factor of √2 occurs because the visual system integrates both signal and uncorrelated noise from the two eyes. This means that the signal increases by a factor of 2, whereas binocular noise amplitude is the square root of the sum of the monocular variances, giving a signal-to-noise ratio of 2:√2 = √2 relative to a single eye. As recognized before (Blake et al., 1981; Campbell & Green 1965), this summation model requires either that the noise from one eye disappears when the signal is in the other eye or that the observer is able to respond selectively to the monocular pathway in the monocular condition.

A binocular summation model of broader scope is that of Legge (1984b). Each monocular pathway passes through an accelerating nonlinearity prior to mandatory binocular summation. The monocular response to contrast (c) is expressed as c^q, and this predicts a $2^{(1/q)}$ improvement for binocular contrast detection. When $q = 2$, this provides a convenient expression for computing monocular contrast energy and, of course, describes the widespread belief that binocular summation is quadratic (e.g., Blake et al., 1981; Smith et al., 1997; Strasburger, 2001).

Binocular interactions above detection threshold

Two eyes are better than one at detection threshold, but this binocular advantage appears to be lost at higher stimulus contrasts. For contrast discrimination, monocular and binocular threshold functions converge at moderate pedestal contrasts and above (Legge, 1984b), perhaps suggesting that there is no binocular summation of contrast above threshold. However, some care is needed here. Although it is clear that there is no empirical difference in contrast increment thresholds for clearly visible monocular and binocular gratings (Legge, 1984b), this does not imply that the process of neural binocular summation is abolished. Rather, Legge's model suggests that for moderate contrasts and above, the binocular advantage of summation is offset by an increase in masking when pedestals (masks) are also presented to both eyes. Thus, this binocular summation paradigm confounds the number of eyes tested with the number of eyes masked. In an effort to disentangle summation and masking, we have devised an approach in which the pedestal is binocular but the test contrast increment may be applied to one eye or to both eyes. We call the novel condition described by the first of these possibilities "half-binocular" (binocular pedestal, monocular test increment).

Scope

Our broader aim is to present a fresh look at the early stages of luminance contrast vision. We investigate the processes of monocular and binocular contrast transduction and binocular interactions by measuring binocular summation and monocular, binocular, and dichoptic masking functions for the same observers. Using these classic paradigms and our novel half-binocular condition (see above), we overturn three long-held views about binocular vision. First, we show that binocular summation is greater than the classical value of √2. Second, we find that contrary to a widely held view, dichoptic masking can produce interocular facilitation at low mask contrasts. Third, our comparison of full- and half-binocular conditions shows that empirical binocular summation is approximately constant across most of the range of pedestal contrasts tested. We show that the first two results are inconsistent with our formulation of Legge's model, as well as another more recent model incorporating interocular suppression (Meese, Georgeson, & Hess, 2004; Meese & Hess, 2004), but we find that two new models provide very good accounts of our data. The first of these is a *two-stage model* of contrast gain control, where the first and second stages receive monocular and binocular excitation, respectively, but divisive suppression is binocular at both stages. The second model was motivated by very recent work of Maehara and Goryo (2005), published while this article was in preparation. The *twin summation model* here is a generalization of their model, modified for the stimuli used in our experiments. This model incorporates monocular nonlinearities and binocular summation within parallel excitatory and inhibitory pathways prior to a single stage of contrast gain control. The two-stage model and the twin summation model both correctly predict several novel effects in the psychometric functions we have measured and explain a previously puzzling pattern of results for contrast matching.

Methods

In all experiments, we used two-interval forced-choice (2IFC) staircase procedures to collect data on contrast detection or contrast discrimination for horizontal sine-wave gratings.

Equipment

Experiments 1 and 2 used a Macintosh G4 computer with PsychToolBox software (www.psychtoolbox.org) running under Matlab 5.2.1. Images were displayed on a Clinton fast-phosphor monitor and were presented separately to the two eyes using CRS ferroelectric goggles with little or no cross talk. Frame rate was 150 Hz (75 Hz per eye). Mean luminance, as seen through the frame-interleaving goggles, was 26 cd/m^2. The system was carefully gamma corrected (linearized), and contrast was controlled, via lookup tables. Pseudo-14-bit grayscale resolution was obtained by using the CRS Bits++ graphical interface in Bits++ mode.

In Experiment 3, stimuli were generated using the framestore of a CRS VSG2/3 operating in twin palette mode to produce pseudo-12-bit gray level resolution. In this mode, up to 256 gray levels are available for every image frame
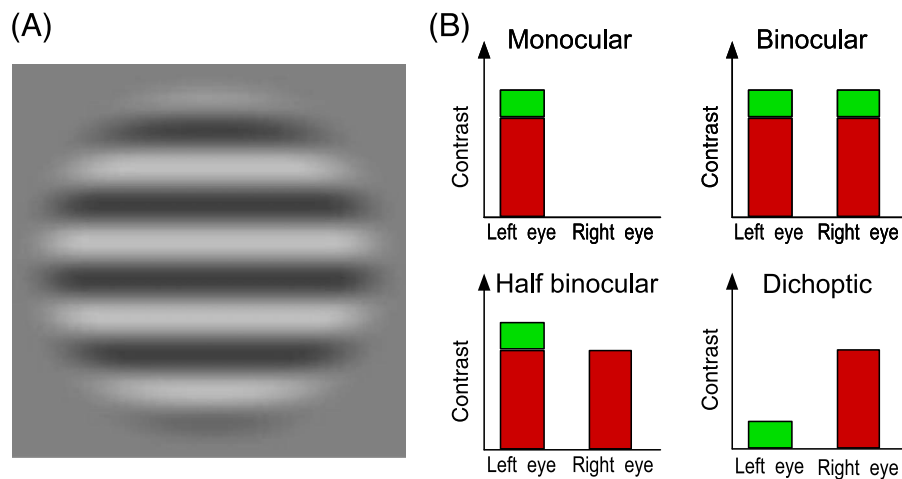
Figure 1. Stimuli. (A) Mask and test stimulus used in all three experiments. (B) The four different configurations for the mask stimulus (red) and test stimulus (green). In the experiments, the test and mask stimuli were counterbalanced across eye.

and are selected from 4,096 discrete levels. Stimuli were presented on an NEC monitor, which had a mean luminance of 60 cd/m^2 and was gamma corrected using lookup tables. The experiments were run under the control of a PC. Stimuli were viewed through a mirror haploscope (four pairs of front-surfaced mirrors, set at $\pm45°$) affording a square field size of $11.5° \times 11.5°$ and an effective viewing distance of 52 cm. The visible region of the display consisted of a 256-pixel square array for each eye. The frame rate of the monitor was 120 Hz, which gave a picture refresh rate of 60 Hz due to frame interleaving across eyes. This was done to allow fine control over the contrast presented to each eye.

In Experiments 1 and 2, a chin rest and a forehead rest were used. In Experiment 3, only a chin rest was used.

Stimuli

The same spatial pattern was used for mask and test stimuli in all of the experiments (see Figure 1A). This was five cycles of a horizontal sine-wave grating with a spatial frequency of 1 cycle per degree. The circular stimulus aperture had a total diameter of 5°, and its outer edge was blurred by half a cycle of a raised sine function subtending 0.5°.

In all experiments, the phase of the stimulus was the same in both presentation intervals of the 2IFC task, and the small central fixation point (2×2 pixels) was visible throughout. In Experiment 3, the grating was always in sine phase (0°) with a central fixation point. In Experiments 1 and 2, the phase of the grating was randomly selected from four quadrature phases (0°, 90°, 180°, and 270°) on each trial.

Stimulus contrast is expressed in percentage, as $c = 100(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are maximum and minimum luminance values, respectively, and also as decibel contrast relative to 1%, equal to $20 \log_{10}(c)$.

Stimulus conditions

There were four ways of stimulating the two eyes (see Figure 1B). In the monocular condition, the mask and test gratings were displayed to the same eye. In the binocular condition, the gratings were displayed to both eyes. In the dichoptic condition, the test was displayed to one eye and the mask to the other eye. In the half-binocular condition, the mask was displayed to both eyes and the test to one eye. In the monocular and dichoptic conditions, the nonstimulated eye was presented with mean luminance. In all conditions, presentations were counterbalanced across eyes. In Experiments 1 and 2, this counterbalancing was performed within experimental sessions (the stimulus levels for the different eyes and types of stimulation were controlled by different interleaved staircases), whereas in Experiment 3, trials for each test eye were blocked.

Procedure for Experiment 1: Binocular summation at threshold

In this experiment, mask contrast was set to 0%. A small, black, 2-min-wide fixation spot was present on screen throughout the session. Experimental sessions consisted of randomly interleaved trials for left-eye stimulation, right-eye stimulation, and binocular stimulation. Four independent staircases were used to track detection performance: two for the monocular conditions and two for a pair of identical binocular conditions, using a three-down, one-up selection rule. Another four staircases, interleaved with the others, used a two-down, one-up rule. The aim here was to spread the sampling of contrast levels to improve the estimation of psychometric slopes. Step size was 2 dB. The staircases terminated after 32 trials each. This arrangement

resulted in equal numbers of (1) monocular and binocular trials and (2) left- and right-eye trials.

Four different stimulus durations (40, 100, 200, and 500 ms) were used in different blocks of trials. The time between stimulus intervals was 500 ms. Pooled across four sessions, each monocular or binocular threshold was derived from 512 trials per duration per subject.

Procedure for Experiment 2: Superimposed masking

In this experiment, stimulus duration was 200 ms and the time between test intervals was 500 ms. A small black fixation point (2×2 pixels) was displayed throughout the session. The 2IFC staircase used a three-down, one-up selection rule with a 2-dB step size. Presentation was blocked by pedestal contrast level, with all three stimulus conditions (monocular, binocular, and dichoptic) interleaved and counterbalanced across eyes within a block. A single independent staircase was used for each of the six configurations (left- and right-eye monocular and dichoptic conditions as well as a pair of identical binocular conditions), which terminated after 50 experimental trials. The data were pooled across eye and six experimental sessions, resulting in 600 trials per stimulus condition for each observer or 1,800 trials for each data point in Figure 3.

Procedure for Experiment 3: Binocular summation above threshold

In this experiment, stimulus duration was 100 ms and the time between test intervals was 500 ms. Four short nonius lines (5 pixels in length) surrounded the stimulus to aid binocular fusion, and along with a 4-pixel square fixation point, they were visible throughout the experiment. The 2IFC staircase used a three-down, one-up selection rule with a 3-dB step size. Five stimulus conditions (left monocular, right monocular, left half-binocular, right half-binocular, and binocular) were performed in randomized blocks for each pedestal contrast, and the whole set of contrasts was repeated four times. When pooled across sessions, this yielded an average of 600 trials per threshold estimate per subject in the monocular and half-binocular test conditions and 306 trials in the binocular test condition.

Threshold estimation

Preliminary analysis showed that for all observers, contrast sensitivity was similar for the two eyes. Therefore, where the test stimulus was displayed to one eye only (monocular, dichoptic, and half-binocular conditions), results were combined across eyes to produce best estimates of threshold. In Experiments 2 and 3, contrast detection and discrimination

thresholds were estimated by collapsing the 2IFC staircase data across replications and fitting a psychometric function ($\psi()$) to proportion correct using a Simplex algorithm and maximum likelihood estimation. In Experiment 1, the psychometric function was fit to the data from each experimental session. In all cases, the psychometric function was a Weibull function given by

$$\psi(\Delta C) = 0.5 + (0.5 - \lambda)(1 - \exp[-(\Delta C/\alpha)^\beta]),$$

where ΔC is the test contrast, α is the detection threshold (81.6% correct when $\lambda = 0$), β is the slope of the psychometric function, and λ is a lapse rate parameter constrained to be ≤ 0.04 to allow for finger errors. The lapse parameter can be important when estimating the slope of the psychometric function (Wichmann & Hill, 2001). In Experiment 1, 13 of the 16 psychometric fits gave an estimated lapse rate of 0. For Experiment 3, λ was fixed at a small value (0.01).

Observers

Two of the authors (T.S.M. and M.A.G.) took part in Experiments 1 and 3. One of the authors (D.H.B.) and two postdoctoral research fellows (D.J.H. and R.J.S.) took part in Experiment 2. All of these observers had normal or corrected-to-normal vision.

Results

Experiment 1: Binocular summation at threshold

Binocular summation ratios were calculated by dividing the monocular detection threshold by the binocular detection threshold; this gives the ratio of binocular to monocular sensitivities. (We also express these ratios in decibels by taking $\log_{10}$ and multiplying by 20.) Binocular summation ratios are shown in Figure 2 for the four different stimulus durations. In all cases, summation is greater than the quadratic prediction of $\sqrt{2}$ (3 dB) but less than a perfect linear summation ratio of 2 (6 dB) and has an average of 1.70 (4.6 dB). In particular, this result is inconsistent with the quadratic summation model of Legge and the ideal linear summation model of Campbell and Green, both of which predict binocular summation ratios of $\sqrt{2}$ (3 dB). Psychometric slopes did not differ significantly between monocular and binocular testing. Mean values (± 1 *SE*, $n = 8$) for slope parameter β were 3.00 ± 0.27 (monocular) and 3.31 ± 0.27 (binocular).

Elsewhere, we report a more extensive investigation of summation at threshold (Georgeson & Meese, 2005) showing that a similarly high degree of summation is found across a wide range of spatiotemporal frequencies (1 to 8 Hz and 1 to 4 cycles per degree). The results here are also confirmed in
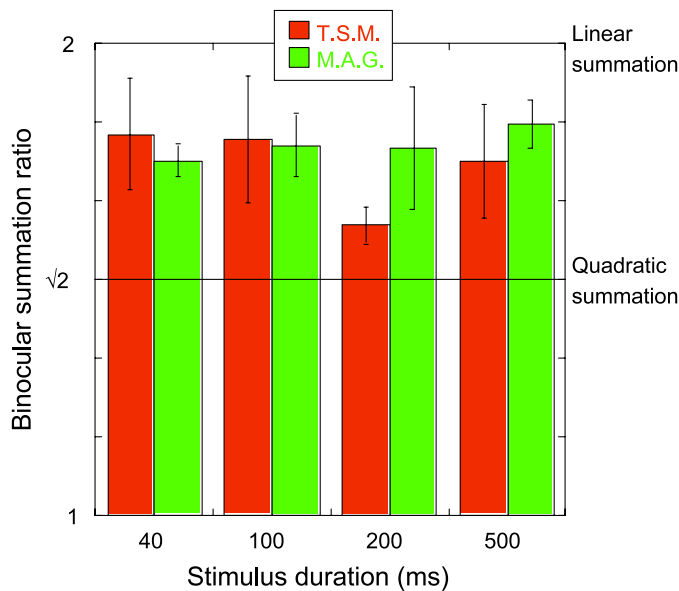
Figure 2. Binocular summation ratios at detection threshold (mask contrast = 0%) for two observers (different shades) from Experiment 1. Summation ratios were calculated as the average monocular threshold divided by the average binocular threshold, and the plot shows the mean and standard error of four such estimates from individual sessions. Each mean ratio is based on results from 2×512 trials. In all cases, the level of binocular summation falls between the predictions for quadratic summation and linear summation. Tick marks represent ratio increments of 1 dB (20 times the $\log_{10}$ ratio), from 0 to 6 dB.

the following two masking experiments where the average binocular summation at threshold (mask contrast = 0%) was 4.5 dB for D.J.H., R.J.S., and D.H.B. (Experiment 2) and 4.8 dB for T.S.M. and M.A.G. (Experiment 3).

Experiment 2: Detection and discrimination thresholds for superimposed masking

Experiment 2 raised the inquiry above basic detection threshold by measuring monocular, binocular, and dichoptic contrast-masking functions across a wide range of mask (pedestal) contrasts. Results were similar for the three observers (D.H.B., D.J.H., and R.J.S.), and their averages are plotted in Figure 3 (95% confidence limits are shown in Panel B). There are several key observations. At low monocular and binocular mask contrasts, facilitation occurs (Nachmias & Sansbury, 1974; Stromeyer & Klein, 1974) but gives way to masking at higher contrasts, producing a classic dipper shape (Legge & Foley, 1980; Wilson, 1980). These two functions reveal binocular summation at very low pedestal contrasts but converge at higher contrasts (around 3%), similar to the findings of Legge (1984b). Notably, though, in the initial region of the dip, binocular summation is greater than or equal to the 4.5 dB

observed at detection threshold. Clearly, a successful model of binocular summation and masking must be consistent not only with the $>\sqrt{2}$ binocular advantage at detection threshold but also with that in the dipper region.

Dichoptic masking is shown by open cross symbols in Figure 3 and is much more severe than in the other two conditions. As in previous studies (Harrad & Hess, 1992; Legge, 1979; Levi, Harwerth, & Smith, 1979; Maehara & Goryo, 2005), the test contrast has to be about as high as the mask contrast to be detected at moderate mask contrasts and above, and the function has a slope close to unity, consistent with Weber's law. (The slopes of the best fitting straight lines through the five highest mask contrasts on double log coordinates were 0.98 for the dichoptic condition but 0.71 and 0.66 for the monocular and binocular cases.) Of particular note is the small region of facilitation produced by the dichoptic mask. This feature was clearly evident in the data of all three observers, and we have replicated it several times for T.S.M. and D.H.B. (not shown), indicating a robust effect. Maximum facilitation for the average observer here (Figure 3) was 4.1 dB for the dichoptic condition, as compared with 9.9 and 8.0 dB for the monocular and binocular conditions, respectively. (This compares favorably with the average of the maximum level of facilitation found for each observer, which was 3.9, 9.7, and 8.3 dB, and shows that the averaging process has not distorted the dipper.) The finding of dichoptic facilitation contrasts with earlier conclusions (Legge, 1979), where dichoptic facilitation was probably missed due to sparse sampling of mask contrasts. There was also some evidence for dichoptic facilitation in the data of Maehara and Goryo (2005), although it was weaker than that seen here. It is possible that the use of mask stimuli with greater spatial extent than the test patch attenuated facilitation in that study, as is known to happen in the binocular case (Foley, 1994; Foley & Chen, 1999; Meese, 2004). Finally, we note that in Levi et al.'s (1979) study on amblyopia, dichoptic facilitation was found for their one normal (control) observer.

To try and understand the visual processes underpinning the various phenomena in Figure 3, we have fit the data with the four different models sketched in Figure 4 and expressed formally in Table 1. The fitting procedure used a downhill simplex algorithm that minimized the squared error of the fit in decibels. The assignment of test and mask contrasts in the models is shown in Figure 1B for the different stimulus configurations.

We extended Legge's quadratic summation model to suprathreshold conditions (Figure 4A) by adding a compressive stage after binocular summation (Legge, 1984b) and generalized it by allowing the monocular exponent q to be a free parameter. The current formulation is the same as the treatment by Meese and Hess (2004; where $q = 2$) and, hereafter, is called the Legge-type model.

For monocular and binocular stimulation, the Legge-type model behaves in the same way as contrast gain control models (Foley, 1994) and fits the dipper shape of contrast-masking functions. As shown by Legge (1984b), it also
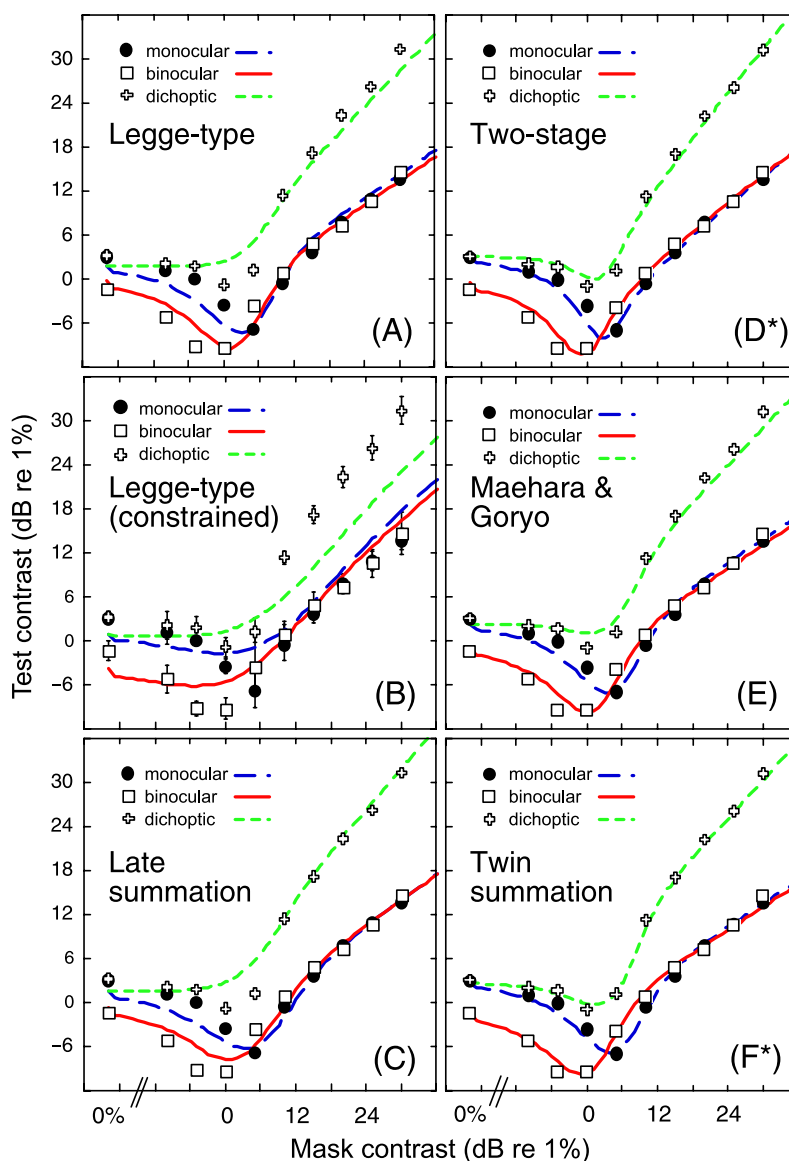
Figure 3. Detection and discrimination thresholds and model fits for Experiment 2 from approximately 54,000 2IFC trials. Data are monocular, binocular, and dichoptic masking functions averaged across three observers (D.H.B., D.J.H. and R.J.S.). (A) Best fit of Legge-type model. (B) Fit of Legge-type model constrained to produce the observed level of binocular summation at detection threshold. (C) Best fit of the late summation model. (D) Best fit of the two-stage model of contrast gain control. (E) Best fit of Maehara and Goryo's model. (F) Best fit of the twin summation model. The asterisks (D* and F*) denote the two models with the best performances (lowest RMS errors). Error bars in Panel B show 90% confidence limits calculated by a bootstrap technique, which estimates the variance both within and between observers after normalizing to overall sensitivity.

approximates the convergence of monocular and binocular masking functions and describes the severe dichoptic masking. Although the overall fit is quite good (RMS error = 1.75 dB), it has two major failings. First, there is a complete absence of dichoptic facilitation. Second, the best fitting value of $q = 3.03$ (see Table 2) results in far too little binocular summation at low mask contrasts. To achieve the level of summation found in these detection data (mask contrast = 0%), the exponent must be reduced to $q = 1.34$. However, this adjustment results in the unfortunate side effects shown in Figure 3B. Specifically, the value of

q controls (1) the depth of the dip in monocular and binocular masking and (2) the separation between monocular and dichoptic masking at high contrasts. With the low value of q needed as described above, both of these features are underestimated. (The second effect occurs because as q approaches 1, the monocular and dichoptic conditions become increasingly similar for this model.) Clearly, the Legge-type model cannot survive in its present form.

A refinement of the Legge-type model was suggested by Meese and Hess (2004) and showed promise in a preliminary examination of some of its features by Meese et al.
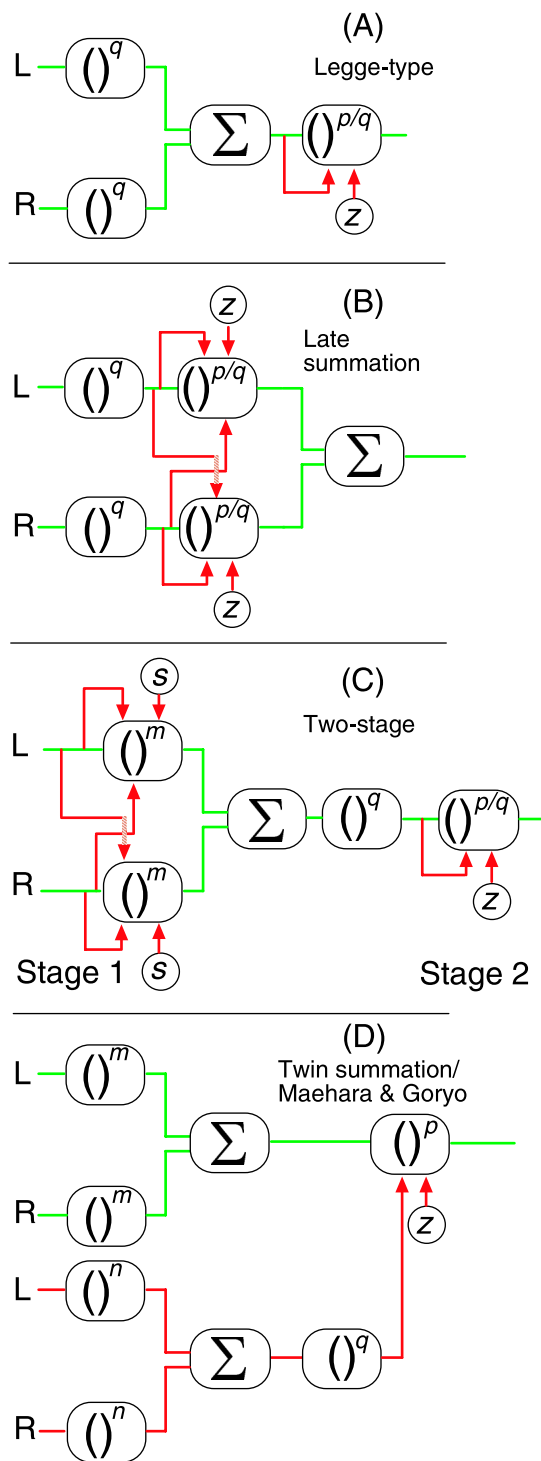
Figure 4. Schematic models of contrast gain control and binocular summation (see Table 1 for model equations). L and R are left- and right-eye contrasts, respectively, at the same spatial frequency and orientation in each eye. Green lines indicate excitatory data lines, red lines indicate suppressive control lines, and the arrows denote divisive input. Not shown is Gaussian noise added to the output of each model. (A) Legge-type model. (B) Late summation model. (C) Two-stage model. (D) Twin summation model (developed from Maehara & Goryo, 2005). The number of free parameters is 4, 4, 6, and 6, respectively (see Tables 1 and 2).

(2004). We refer to this model as the late summation model because interocular suppression and contrast gain control are placed before binocular summation (Figure 4B). However, this model offers only marginal improvement in the quality of fit over the Legge-type model for the data set here (see Table 2), and the two models share common failings (cf. Figures 3A and 3C).

Much better predictions were obtained from the novel two-stage contrast gain control model of Figure 4C. Here, the excitatory exponent of the first monocular stage is low ($m = 1.28$) and, thus, binocular summation is high, but dichoptic masking remains severe due to the inclusion of interocular suppression (with the interocular suppression removed, the model reverts to behavior like that in Figure 3B when refit to the data; Georgeson, Meese, & Baker, 2005). The model also captures all the other main features of the data including the different levels of facilitation in each of the three conditions and the convergence of monocular and binocular masking functions (see Figure 4C). In particular, the second-stage excitatory exponent (p) allows for deeper regions of facilitation than would be seen with only a first-stage transducer, where $m = 1.28$.

Fourthly, we consider the model introduced by Maehara and Goryo (2005). Their formulation involved different sensitivities to mask and test contrasts on both the numerator and denominator of a contrast gain control equation (i.e., four sensitivity parameters). However, for the stimuli used here, this formulation is inappropriate because the mask and test are spatially identical and so must have the same sensitivity. A schematic illustration of our modification and generalization of Maehara and Goryo's model is shown in Figure 4D. The model equation is shown in Table 1. In Maehara and Goryo's original model, $m = p$ and $n = q$, and a fit of the model with this constraint is shown in Figure 3E. Of the three different four-parameter models we have tried, this model undoubtedly produces the best overall fit (see Table 2). However, it does not produce a sufficiently marked dip in the dichoptic condition and it tends to underestimate binocular summation at low mask contrasts. This model's behavior falls somewhere between the Legge-type model and the two-stage model. We were able to improve upon this with the more general, six-parameter, *twin summation model* (Table 1). The fit is shown in Figure 3F and captures all features of the data very well. (We also tried a five-parameter version with the constraint $p = q$. This performed very well [RMS error = 0.76 dB] but slightly underestimated the level of dichoptic facilitation.)

Experiment 2: Psychometric slopes for superimposed masking

Until now, we have restricted our analysis to detection and discrimination thresholds. However, these assess the models at just a single level of performance on the psychometric function (e.g., 81.6% correct in our experiments). In fact, the model equations allow sensitivities to

Model name		Equation		Data figure (Figure 3 panel)	Model figure (Figure 4 panel)
Legge-type	(1)	$\text{resp}(L,R) = \dfrac{(L^q + R^q)^{p/q}}{z + L^q + R^q}$		A and B	A
Late summation	(2)	$\text{resp}(L,R) = \dfrac{L^p + R^p}{z + L^q + R^q}$		C	B
Two-stage gain control	(3)	$\text{Stage1}(L) = \dfrac{L^m}{s + L + R}, \quad \text{Stage1}(R) = \dfrac{R^m}{s + L + R}$		D*	C
		$\text{resp}(L,R) = \dfrac{(\text{Stage1}[L] + \text{Stage1}[R])^p}{z + (\text{Stage1}[L] + \text{Stage1}[R])^q}$			
Twin summation/Maehara and Goryo	(4)	$\text{resp}(L,R) = \dfrac{(L^m + R^m)^p}{z + (L^n + R^n)^q}$		E and F*	D
Decision variable Δr, (all models)	(5)	$\Delta r = \text{resp}(L_{\text{mask}} + L_{\text{test}}, R_{\text{mask}} + R_{\text{test}})$ $-\text{resp}(L_{\text{mask}}, R_{\text{mask}})$			

Table 1. Model equations. *L* and *R* are the contrasts in the left and right eyes, respectively. For example, in the binocular condition, *L* = *R*, whereas in the monocular condition, either *L* = 0 or *R* = 0. The asterisks (D* and F*) denote the two models with the best fit. All models have late additive noise, consistent with the last equation in this table. Note that the standard deviation of the noise (σ) was unknown and, therefore, a free parameter in all models. Alternatively, this free parameter can be thought of as the output gain of the detecting mechanism.

be derived for a full range of performance levels, which means that predictions for the slopes of the psychometric functions can also be made as follows.

In fitting the models, parameters (*m, n, s, p, q*, and *z*, as appropriate) were adjusted so that the difference in responses between test and nontest intervals (Δr) was equal to a constant (across mask contrasts and test conditions) related to the standard deviation of late additive noise (σ). As the value of σ was unknown, it was a free parameter in the model (see Tables 1 and 2). For 2IFC, signal detection theory shows that percent correct is equal to $\Phi(d'/\sqrt{2})$, where $\Phi()$ is the standard normal integral. From this, it follows that 81.6% correct ("threshold") corresponds to d' = 1.273. Because, by definition, $d' = \Delta r/\sigma$, it follows that $\sigma = \Delta r/1.273$. To produce the model psychometric functions, $\Psi(\Delta C)$, we calculated percent correct as $\Phi(\Delta r/(\sigma\sqrt{2}))$ for a

range of values of ΔC (threshold, ±15 dB). Slopes of these model psychometric functions were derived by fitting Weibull functions, $\hat{\Psi}(\Delta C)$, given by

$$\hat{\Psi}(\Delta C) = 0.5 + 0.5(1 - \exp[-(\Delta C/\alpha)^\beta]),$$

where α is the test contrast corresponding to 81.6% correct (threshold) and β is the slope of the psychometric function.

Empirical slopes and model slopes are shown in Figure 5. For both monocular and binocular stimulation, empirical psychometric slope is quite steep at detection threshold but soon becomes shallow at higher contrasts due to the linearizing effect of the pedestal for the detection of small signals. This occurs because the nonlinear contrast response function is approximately linear over the small increments needed for discrimination above threshold. This

Model name	Data figure (Figure 3 panel)	Model figure (Figure 4 panel)	Free parameters	RMS error (dB)	*m*	*n*	*s*	*p*	*q*	*z*	σ	B_{sum} (dB) = 4.5
Legge-type	A	A	4	1.75	–	–	–	3.47	**3.03**	4.76	0.250	2.0
Legge-type (constrained)	B	A	3	3.68	–	–	–	1.67	**1.34** (Fixed)	3.38	0.207	4.5
Late summation	C	B	4	1.66	–	–	–	**2.76**	2.34	4.59	0.212	2.1
Two-stage	D*	C	6	0.873	**1.28**	–	0.985	7.99	6.59	0.077	0.194	3.5
Maehara and Goryo (constrained)	E	D	4	1.17	= *p*	= *q*	–	**1.88**	1.75	6.036	0.255	3.2
Twin summation	F*	D	6	0.664	**1.43**	1.28	–	2.47	2.4	7.06	0.259	4.0

Table 2. Parameter values and other details for the four models in Figure 4 and two constrained versions of those models. Values were produced by the six fits shown in Figure 3 for Experiment 2. The parameters in boldface are the excitatory monocular exponents prior to binocular summation and play a key role (in some cases, sole role) in controlling the level of binocular summation. B_{sum} is the model's level of binocular summation at detection threshold. The value in the title row indicates the empirical estimate from Experiment 2. The asterisks (D* and F*) denote the two models with the best performances (lowest RMS errors).
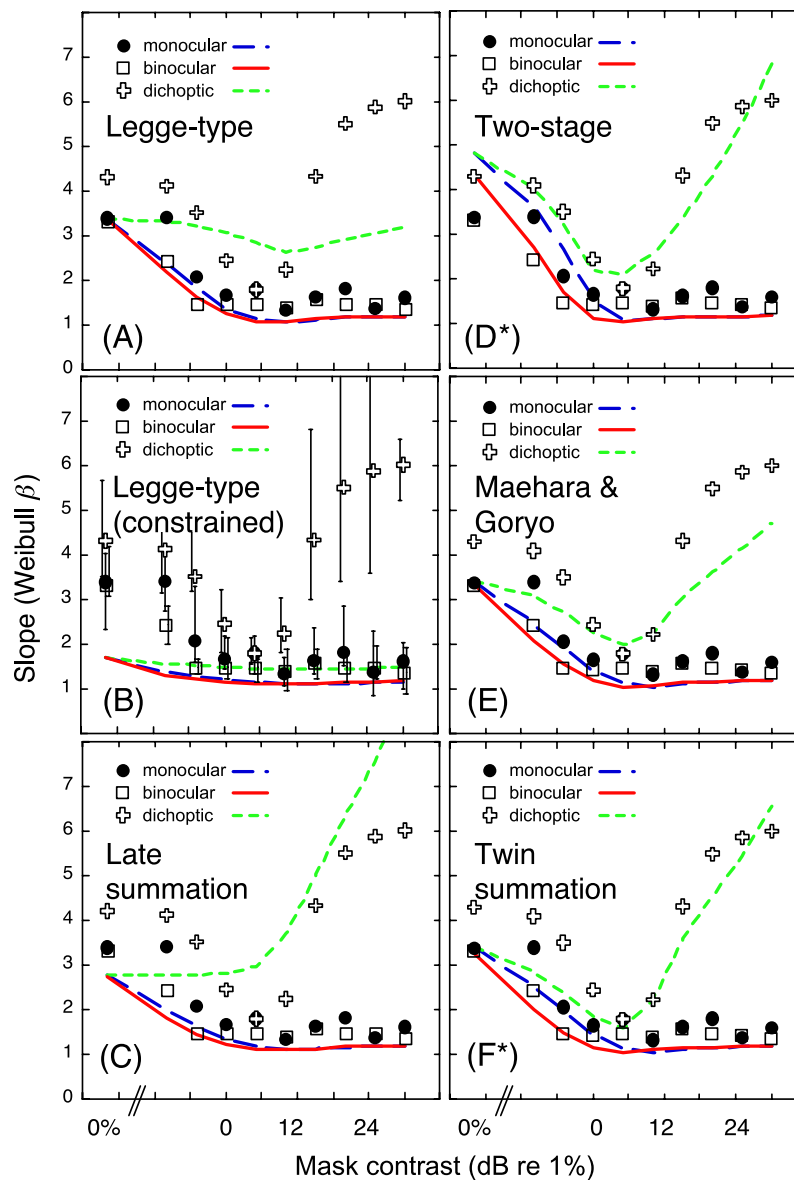
Figure 5. Psychometric slopes and model predictions for Experiment 2. Data are median (*n* = 18) psychometric slopes (Weibull parameter β) pooled across eye (100 trials), for monocular, binocular, and dichoptic masking functions from three observers and six replications. Model curves are predictions with all parameters determined by the fits to the discrimination data in Figure 3 (i.e., there are no free parameters). Predictions are for (A) Legge-type model, (B) constrained Legge-type model, (C) late summation model, (D) two-stage model, (E) Maehara & Goryo model, and (F) twin summation model. The asterisks (D* and F*) denote the two models with the best fits to the discrimination data (lowest RMS errors) in Figure 3. The error bars (B) show 90% confidence limits calculated by a bootstrapping technique.

finding extends a well-established result for binocular stimulation (Bird, Henning, & Wichmann, 2002; Foley & Legge, 1981; Georgeson & Meese, 2004; Legge, Kersten, & Burgess, 1987) to the monocular case. The predictions of the Legge-type model work quite well for these conditions (Figure 5A) because of the model's accelerating nonlinear response at detection threshold and the pedestal effect above threshold (Bird et al., 2002; Georgeson & Meese, 2004).

For the dichoptic mask, the pattern of slopes (Figure 5) is very different from those described above. As contrast increases, the slopes begin steep, become shallow (but at a higher mask contrast than for monocular and binocular con-

ditions), and then become much steeper ($\beta \sim 6$). This is broadly consistent with previous evidence for super-steep psychometric slopes for high-contrast dichoptic masks (Meese et al., 2004). Psychometric slopes also become very steep when stimulus uncertainty is a strong factor. For example, Meese, Hess, and Williams (2001) found an average $\beta = 5.7$ for three uncertain observers in a contrast discrimination task well above detection threshold. However, as the dichoptic mask should reduce, rather than increase, uncertainty, it is unlikely that uncertainty is responsible for the effects we have observed here. Instead, we look for this as an emergent property of the models we are testing.

The Legge-type model (Figure 5A, short, green, dashed curve) fails the test badly. Neither the fall nor subsequent rise in slope is anticipated, and parameter manipulation could not improve notably on this performance. In sum, the Legge-type model not only fails to capture important details of the threshold data (see previous subsection) but also fails to describe gross effects in the psychometric slopes.

For completeness, we also show the predictions for the constrained Legge-type model in Figure 5B. They are very poor.

The late summation model (Figure 5C) predicts very steep psychometric slopes for high-contrast dichoptic masks and moderate steepness at detection threshold. However, it is clear that this model does not describe the complete pattern of psychometric slopes across the range of dichoptic mask contrasts tested here.

The two-stage model (Figure 5D) predicts all the key features of the psychometric slope data remarkably well.

Predictions for Maehara and Goryo's (2005) model (Figure 5E) are in fair qualitative agreement with the empirical estimates but underestimate steepness at high dichoptic mask contrast. Predictions for the twin summation model (Figure 5F) are very good. Of particular note is that this model predicts slightly shallower psychometric functions than the two-stage model at detection threshold, consistent with the data. We also note that unlike the two-stage model, predicted psychometric slopes are identical for monocular and binocular conditions at contrast detection threshold (mask contrast = 0%). Other studies that have made this comparison empirically have also come to this view (e.g., Georgeson & Meese, 2005; Legge, 1984a), although it is not clear that there is sufficient accuracy in the empirical estimates to draw firm conclusions on the matter (Legge, 1984a).

In sum, the two-stage model and the twin summation model not only provide the best fits to the discrimination thresholds (Figure 3), but also, with all parameters fixed by this procedure, provide the best predictions for the psychometric slopes from the same experiment.

Legge and Rubin's (1981) experiment: Contrast matching

A long-standing issue in spatial vision is whether a single contrast response function, $R(c)$, can account for both contrast discrimination and contrast matching. The neural codes for these two tasks are not necessarily closely related, but a model for contrast coding that did account for both would have greater power and generality. In a unified scheme, we should expect discrimination to be related to both the derivative dR/dc and the noise σ, as above, whereas matching could depend solely on the mean R. We thus challenged our models, based on discrimination data, to predict the contrast-matching data of Legge and Rubin (1981). In their experiment, observers adjusted the overall contrast of a dichoptic test stimulus, which had different contrasts in the two eyes, to match a binocular standard of fixed contrast

(see figure caption for experimental details). Typical results for one of their observers (G.R.) are replotted in Figure 6 for four different standard contrasts. Note that the left- and right-eye contrast axes for the dichoptic test stimulus are normalized by the contrast of the standard. There are two notable features of the data. First, proportionally higher dichoptic contrasts are needed to match the low-contrast binocular standards (open symbols), as compared with the high-contrast binocular standards (filled symbols). Second, there is a tendency for the matching functions to curve back in on themselves as they approach the monocular axes, although this effect is clearer for the right eye than the left eye.

We supposed that the contrasts appear to match when the binocular response to the dichoptic test stimulus is equal to that for the binocular standard, and we calculated this numerically for each of the models. Model predictions are shown in the different panels of Figure 6. Predictions from the best fit of the Legge-type model to the earlier discrimination data ($q = 3.03$) are shown in Figure 6A. The model loosely describes the general curvature in the data but fails to capture the dependence on standard contrast level. Predictions for the quadratic summation model ($q = 2$ in the Legge-type model)[1] are shown in Figure 6B. As recognized by Legge and Rubin (1981), the curvature is less tight for lower exponents of the monocular transducer (cf. Figures 6A and 6B), but there is no exponent that will cause the curves to distinguish between the different binocular contrasts or to fold back on themselves.

One model rejected by Legge and Rubin (1981) was the *binocular averaging rule,* equivalent to the linear sum of the contrasts in the two eyes (and equivalent to $q = 1$ in the Legge-type model here). This predicts that all of the data should fall on a straight oblique line from the top left to the bottom right of the plots (not shown). Clearly, this model does not describe the data. This is noteworthy because the threshold model of Campbell and Green (1965) also assumes linear summation of monocular contrasts (see Introduction section), and thus, that model does not extend to suprathreshold conditions in a straightforward way.

The behavior of the late binocular summation model is shown in Figure 6C. This model predicts the separation of the data into high and low binocular contrast groups (filled and open symbols), but for all four binocular contrasts, its curvature is too tight.

Predictions for the two-stage model, the Maehara and Goryo (2005) model, and the twin summation model are shown in Figures 6D–F, respectively. All of these models do a fair job in predicting the separation and location of the two data groups.

An emergent property of several of the more successful models above is that they predict the fold-back of the matching functions close to the monocular axes. This is the luminance contrast equivalent of Fechner's paradox. It indicates that when there is a large imbalance in the contrasts presented to the two eyes, perceived contrast will increase if the lower of the two contrasts is decreased to
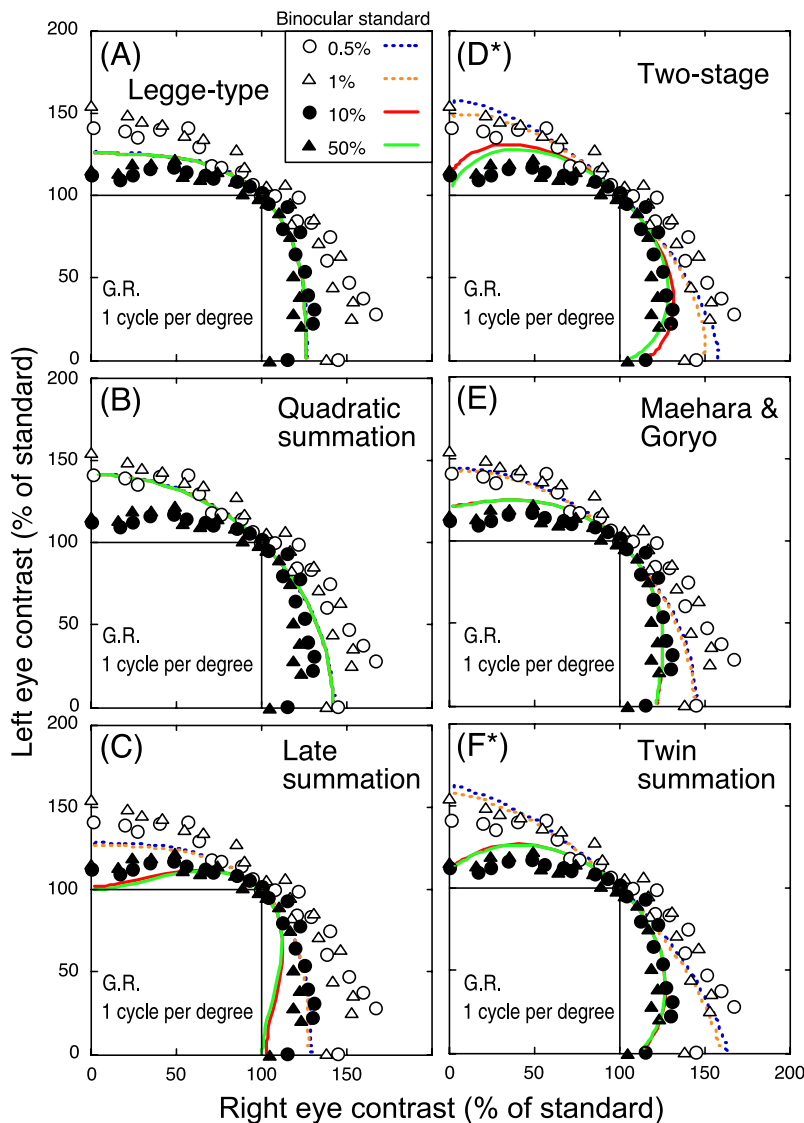
Figure 6. Contrast-matching functions for observer G.R. from Legge and Rubin (1981). Stimuli were 1 cycle per degree sine-wave gratings (width, 12°; height, 20°; duration, 180 ms; and mean luminance, 10 cd/m²). Different panels show model predictions for the models of Figure 4: (A) Legge-type model, (B) quadratic summation model ($q = 2$ in the Legge-type model), (C) late summation model, (D) two-stage model, (E) Maehara and Goryo's (2005) model and (F) twin summation model. Asterisks (D* and F*) denote the two models with the best fits to the discrimination data (lowest RMS errors) in Experiment 2 (Figure 3).

zero. This paradox is most easily understood in the context of the two-stage model (Figure 4). Suppose that the left eye is presented with a high-contrast stimulus (say 50%). As the contrast of a similar stimulus in the right increases, it will contribute to both suppression of and summation with the contrast in the left eye. For low to intermediate contrasts in the right eye, the level of suppression turns out to be greater than the contribution to summation and the overall response decreases. Hence, if the contrast in the right eye is reset to zero, the overall response goes back up again and perceived contrast increases, explaining the paradox.

The paradox also has implications for contrast discrimination in dichoptic masking. In the example above, suppose the fixed left-eye contrast is a dichoptic mask and the var-

iable right-eye contrast is test contrast. As test contrast increases from 0%, the overall response will first decrease before increasing to detection threshold and above. This predicts that performance should drop below 50% correct (a negative d') in the initial region of the 2IFC psychometric function. That is, the psychometric function should be nonmonotonic for dichoptic masking. This is unlikely to have compromised our results in Experiment 2 because the staircase procedure would have steered the test stimulus levels away from the paradoxical effect. However, we have tested the prediction by using the method of constant stimuli to measure psychometric functions over a wide range of test contrasts. Our preliminary investigation has revealed good evidence for this paradoxical effect for high-contrast
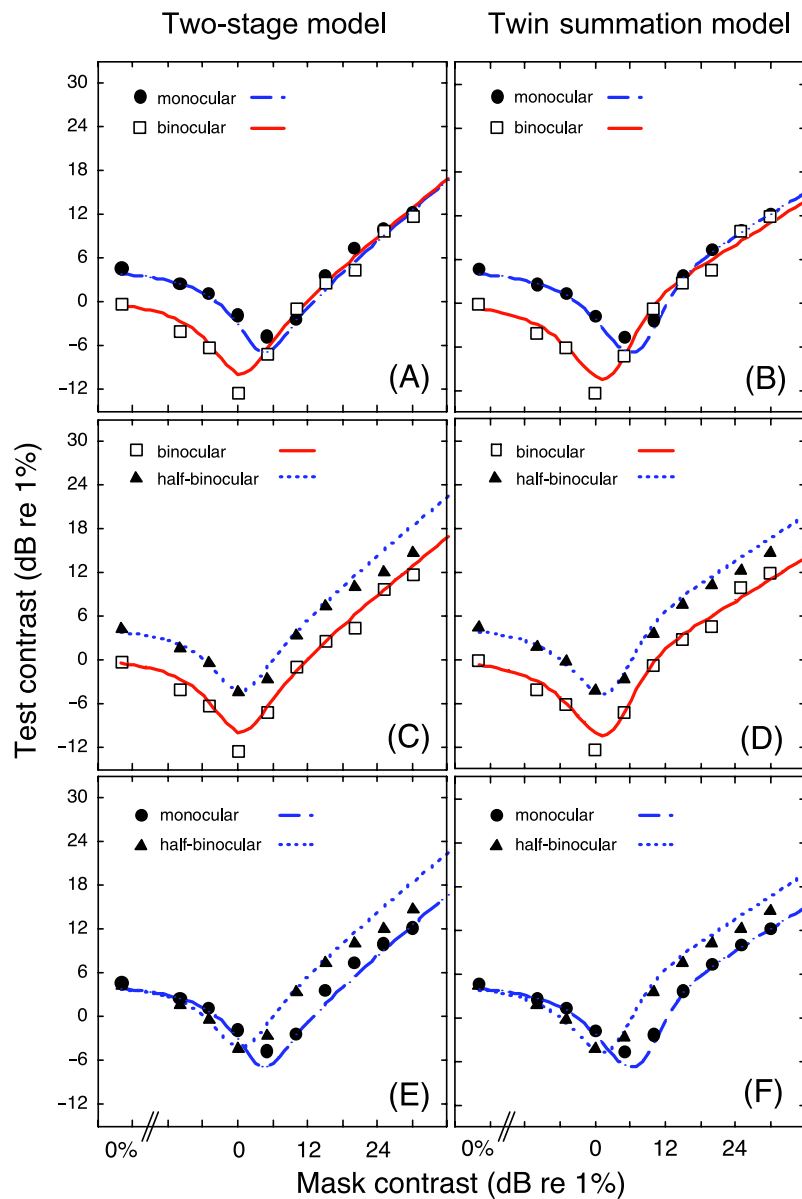
Figure 7. Detection and discrimination thresholds and model behaviors for Experiment 3. Mean monocular, binocular, and half-binocular discrimination thresholds from two observers (M.A.G. and T.S.M.) and four replications. Left and right columns show the behavior of the two best models, and different rows show pairwise comparisons of the three stimulus conditions. For the monocular and binocular conditions, the curves are model fits (see Table 3 for parameters), whereas for the half-binocular condition, the curves are model predictions with no free parameters.

dichoptic masks (Meese, Georgeson, & Baker, 2005), and this issue is continuing to receive our attention.

Experiment 3: Binocular summation above threshold

The traditional approach to binocular summation above threshold is to compare monocular and binocular masking functions, but as we outlined in the Introduction section, this confounds the number of eyes tested with the number of eyes masked. Here, we addressed this problem by devising a "half-binocular" condition in which the mask was presented to both eyes and the test was presented to just

one. We began by fitting the two-stage model and the twin summation model to fresh results (averaged across T.S.M. and M.A.G.) from conventional monocular and binocular conditions (Figures 7A and 7B). The results from these conditions replicate those from two of the conditions in Experiment 2, and the new fits of both models are very good. With the model parameters set (see Table 3), we then made predictions for the new half-binocular condition. In Figures 7C and 7D, the experimental results and model behaviors are compared for the binocular and half-binocular conditions. It is clear that when measured this way, empirical binocular summation extends across the full range of mask contrasts, the average level of summation being 5.1 dB. This compares favorably with the average

	Data figure (Figure 7) panel	Model figure (Figure 3) panel	Free parameters	RMS error (dB) 2 funcs	RMS error (dB) 3 funcs	m	n	s	p	q	z	σ	B_{sum} (dB) = 4.8
Legge type	–	A	4	1.65	1.54	–	–	–	2.61	**2.21**	6.41	0.252	2.5
Late summation	–	B	4	1.92	1.72	–	–	–	**3.13**	2.66	7.08	0.233	2.0
Two-stage	A, C, and E	C	6	1.22	1.36	**1.24**	–	1.42	7.67	6.10	0.062	0.158	4.2
Maehara and Goryo (constrained)	–	D	4	1.33	1.27	= p	= q	–	**1.81**	1.67	8.68	0.247	3.55
Twin summation	B, D, and F	D	6	0.95	1.01	**1.37**	1.28	–	2.9	2.71	7.06	0.259	4.7

Table 3. Parameters and other details for five models fit to results from Experiment 3. The RMS error for "2 funcs" refers to the fits to the conventional monocular and binocular conditions. The RMS error for "3 funcs" refers to the overall error when the half-binocular condition was included in the error calculation but with no further fitting. The parameters in boldface are the excitatory monocular exponents prior to binocular summation, and they play a key role in controlling the level of binocular summation. B_{sum} is the level of binocular summation at detection threshold. The value in the title row indicates the empirical estimate.

predicted levels of 5.2 and 5.3 dB for the two-stage model and twin summation model, respectively. More generally, the models do a good job in predicting overall behavior for the new condition, there being negligible drops in the quality of fit when the half-binocular data are added to the analysis (compare the "2 funcs" and "3 funcs" RMS error columns in Table 3). It is quite striking that despite their numerous nonlinearities, both models predict the almost linear summation of contrast seen across most of the range.

As might be expected from the analyses of Experiments 1 and 2, the Legge-type model, the late summation model, and the Maehara and Goryo model all showed consistent underestimation of binocular summation at threshold for this data set. However, each of these models did predict a substantial difference between the binocular and half-binocular conditions at higher mask contrasts. For completeness, we include the results of the analysis for these models in Table 3.

It is also instructive to compare the half-binocular results with the monocular results as shown in Figures 7E and 7F. This shows that the addition of a dichoptic mask to the monocular condition (see Figure 1B) increased masking by about a factor of 2 just after the half-binocular dip, where it remained for the entire mask contrast range. It is noteworthy that our parameter-free predictions for the half-binocular condition anticipate the crossover of the two functions just to the left of the monocular dip.

One last point concerning masking is as follows. The half-binocular condition is equivalent to a dichoptic condition with an extra mask (pedestal) in the monocular (test) channel. However, dichoptic masking is much more severe than half-binocular masking (cf. Figures 3 and 7), although the half-binocular condition contains greater mask energy across the eyes. Similar results have also been found when the mask and test do not excite the same detecting mechanism (Baker & Meese, 2006b; Meese & Hess, 2005). It is not simple to describe why this happens in the models for the situation here, but it involves a complex interplay between a pedestal effect, monocular masking, dichoptic masking, and binocular summation (between pedestal, test, and dichoptic mask).

In this experiment, the stimulus conditions were blocked, whereas in Experiment 1, a subset of three of these conditions (left- and right-eye monocular and binocular) was interleaved and phase was randomized across trials (see Methods section). Nevertheless, the level of binocular summation at threshold for corresponding conditions (100 ms duration) was identical in both cases (4.8 dB, average for T.S.M. and M.A.G.). This shows that the same result is found irrespective of whether the exact requirements for the ideal observer (that the signal is known exactly) are met. A similar finding has been made recently for spatial summation at threshold (Meese, Hess, & Williams, 2005).

Discussion

In a series of masking and detection experiments, we reexamined binocular interactions for spatially identical patterns of luminance contrast in the two eyes. We found that several previous models did not provide an adequate account of detection and discrimination thresholds (dipper functions), but two new models (the two-stage model and the twin summation model) both performed very well across a wide range of conditions. These two models also account for (1) previously published data on contrast matching, including a contrast version of Fechner's paradox; (2) a complex set of data on the steepness of psychometric functions; and (3) the empirical finding of substantial binocular summation across a wide range of binocular mask contrasts.

Physiological and probability summation of binocular luminance contrasts

All our models include an obligatory stage of linear summation of the two monocular contrast responses, a process sometimes referred to as physiological summation. An alternative form of summation is probability summation, and this has been proposed as a possible form of binocular

summation (see Blake & Fox, 1973, for some discussion). Under the assumptions of high threshold theory (Graham, 1989), this would predict $20 \log_{10}(2^{1/\beta})$ dB of binocular summation, where β is the Weibull slope parameter of the psychometric function (Quick, 1974), assuming equal sensitivity of the two eyes. From Experiment 2, we estimate slope $\beta = 3.61$ at detection threshold, predicting 1.66 dB of summation, considerably less than the 4.5 dB of summation found empirically (Table 1). Within this framework, a much lower value of $\beta = 1.33$ would be required to meet the observed level of summation. However, the assumptions of high threshold theory have long been discredited (e.g., Nachmias, 1981), and in any case, they do not readily extend to suprathreshold conditions (Experiment 3); hence, this account will not suffice on any grounds.

Probability summation can, however, be recast within a signal detection framework. Tyler and Chen (2000) assumed that observers base their decision on the maximum response of the channels monitored across the two intervals, and they varied the number of channels assumed to be monitored for both component and compound stimuli. For a linear transducer and additive noise, most of the situations they considered predicted fourth-root summation or less. This gives a maximum level of $20 \log_{10}(2^{1/4}) = 1.5$ dB for binocular summation by probability summation (or "attentional summation" as Tyler and Chen prefer to call it). Changing the base level of uncertainty or, equivalently, introducing an accelerating nonlinearity, does not change this conclusion appreciably. Some situations that did predict substantially higher levels of summation than the fourth-root rule were found (see Figure 11a in Tyler & Chen, 2000), but they produced psychometric slopes that were far too shallow compared with our data. Thus, probability summation cannot account for binocular summation.

Another alternative to the obligatory summation of monocular responses is a conditional form of summation: The ideal observer would optimize performance by summing responses from the two eyes when the stimulus was binocular and would use the appropriate monocular response when the input was monocular. The Appendix shows that this ideal observer predicts markedly less binocular summation than we observed in the experiments. This ideal observer benefits by selectively excluding noninformative noise (from the other eye) in monocular trials and, as a result, gains less benefit from binocular input than an observer who cannot do this. The high degree of binocular summation that we observe thus points toward obligatory summation of monocular responses.

Uncertainty and noise

The models in Figure 4 assume late additive noise, no uncertainty, and nonlinear (accelerating) contrast response around threshold, all of which are debatable. Recent analysis on the slope and shape of the psychometric function has argued the case for multiplicative noise (Kontsevich, Chen, & Tyler, 2002), but a subsequent analysis of the same data concluded that the additive noise model remains viable (Georgeson & Meese, 2006). A totally different approach involving a category-rating task suggests that the additive noise model is to be preferred (Katkov, Gan, Tsodyks, & Sagi, 2005; see also Katkov, Tsodyks, & Sagi, 2006). Here, we have supposed additive noise because of its simplicity. On this assumption, the compression of signal-to-noise ratio at higher mask contrasts derives from the divisive form of the contrast gain control, but an increase in noise (multiplicative noise) would have the same effect. One might suppose that dichoptic contrast-matching data would go some way toward resolving this because a contrast match is affected only by the mean response and not by the noise level. However, as we pointed out in Footnote 1, the match is independent of the nonlinearities (and noise) placed after binocular summation, and hence, later stages remain possible sites for the injection of signal dependent noise.

Like several other investigators, we have attributed the region of facilitation (the dip) in our masking functions to an accelerating contrast response close to threshold (Legge & Foley, 1980; Nachmias & Sansbury, 1974; Stromeyer & Klein, 1974; Wilson, 1980), but an alternative view is to suppose a linear transducer and an observer who is uncertain about which visual channels to monitor (McIlhagga, 2004; Petrov, Verghese, & McKee, 2006; Tyler & Chen, 2000). On this model, a low-contrast pedestal reduces the uncertainty and facilitation occurs (Lasley & Cohn, 1981; Pelli, 1985; Tyler & Chen, 2000; Yang & Makous, 1995). This model also describes the finding that a low-contrast pedestal will reduce the slope of the psychometric function, as we found in Experiment 2 (Pelli, 1985; Tyler & Chen, 2000).

However, it can be argued that uncertainty is not responsible for pedestal facilitation in general (Kontsevich & Tyler, 1999; Legge et al., 1987). Furthermore, with the assumption of linear transduction and no interactions prior to linear binocular summation and subsequent detection, the uncertainty reduction by the pedestal should be the same in the monocular and dichoptic conditions here. Hence, the above form of the uncertainty model cannot account for the very different levels of facilitation in monocular and dichoptic masking. Nevertheless, we acknowledge that some of what we attribute to an accelerating contrast response might be recast in terms of stimulus uncertainty.

Dichoptic masking

To clarify our terminology, we use the terms "facilitation" and "masking" to refer to empirical effects: the lowering and raising of detection thresholds by a mask, respectively. We use the terms "transducer," "suppression," "divisive inhibition," and "contrast gain control" to refer to the processes or mechanisms that underlie those effects. Specifically, contrast gain control is the setting of a target

mechanism's gain according to the contrast responses of a pool of mechanisms including the target mechanism (Heeger, 1992). One way that this can be achieved is through divisive inhibition, in which case a mask can be said to suppress the response to a test stimulus. When the mask and test are spatially identical, contemporary contrast gain control equations are equivalent to an s-shaped static transducer that describes the operating characteristic (a plot of input vs. output) of the detection mechanism (Legge & Foley, 1980; Wilson, 1980).

A distinct feature of our dichoptic masking results is the region of facilitation. Although not as large as in the monocular and binocular cases, it was clearly evident in all the observers we tested. This result contributed to the rejection of the Legge-type model and the late summation model but was an emergent property of our two most successful models. In those models, it occurs for the same reason as in the better known binocular case; low-contrast masks drive the overall contrast response into a region of acceleration and greater discriminability.

Early work attributed dichoptic masking to early "within-channel" stimulation, essentially the same process as attributed to monocular and binocular masking (Legge, 1979). Although the static transducer model of that time is no longer a viable model of spatial vision (Foley, 1994; Ross & Speed, 1991), a feature of contemporary models of contrast gain control is self-suppression (e.g., Figure 4A), and this can have identical masking effects. For the mask to suppress the test stimulus via self-suppression, it must also excite the same pathway as the test, and thus, for this reason, we continue to use the term within-channel masking. The old view that dichoptic masking arises from within-channel stimulation (Harris & Willis, 2001; McKee, Bravo, Taylor, & Legge, 1994; Westendorf, 1989) was supported by the finding that it is tightly tuned for spatial frequency (Legge, 1979; Levi et al., 1979) and orientation (Harrad & Hess, 1992; Levi et al., 1979), although the substantial effects in the skirts of these functions (~6 dB) tended to be overlooked. More recently, the generality of the within-channel view of dichoptic masking has been challenged. Meese and Hess (2004) performed contrast-matching experiments with briefly presented stimuli (200 ms) and used dichoptic masks with sufficiently different orientation and spatial frequency from the test for them not to excite the same detecting mechanisms (Holmes & Meese, 2004). They found that the masks could attenuate the perceived contrast of a central patch of test grating, when the mask was superimposed or in an annular configuration. Petrov and McKee (2006) used co-oriented annular masks and found them to raise detection thresholds for both monocular and dichoptic presentations in the periphery. All these suggest that dichoptic masking might be a form of suppressive interocular contrast gain control, similar to that proposed for other situations (Foley, 1994; Heeger, 1992; Webb et al., 2003; see also Tyler & Kontsevich, 2005).

Here, we have extended that idea from the cross-oriented or annular cases reviewed above, to the superimposed, spa-tially matched dichoptic masking studied in our experiments here. The two-stage model achieves this with an explicit route for interocular suppression at Stage 1 (Figure 4C). However, the *direct effect* of suppression from the mask on the test is not the only factor involved; there is also an *indirect effect*, caused by suppression from the test on the mask, because the test contrast is so high. This causes the response to the mask to be less in the test interval (test + mask stimulus) than in the null interval (mask alone), and hence, greater test contrast is needed to overcome this. Explorations with the model confirm that both of these factors are important. If the pathway for the eye carrying the dichoptic mask is "lesioned" just before binocular summation, then binocular summation of mask and test does not occur and the indirect effect cannot be a factor. When this is done, dichoptic masking remains but (1) there is no facilitation, (2) masking occurs at much lower mask contrasts, and (3) the masking function is much less steep (the log–log slope drops from 1 to about 0.6). The masking in the lesioned model is due to the direct effect, and the drop in masking at the higher mask contrasts illustrates the contribution of the indirect effect when the model is intact.

One future challenge is to determine whether model lesions of this kind can shed light on the abnormal suppressive effects seen in amblyopia (Harrad & Hess, 1992; Leonards & Sireteanu, 1993; Levi, 1985; Levi et al., 1979; Pardhan & Gilchrist, 1992; Pardhan & Whitaker, 2003).

Which model is best?

One of the most surprising outcomes of the present work is that despite the differences in architecture (Figure 4) and formal expression (Table 1), the two-stage model and the twin summation model behave very much alike in all of the tests we have made. Thus, if matching and masking experiments with spatially matched test and mask stimuli cannot distinguish between the models (see also Baker, Meese, & Georgeson, 2005, in press), are there any other bases upon which one model might be favored over the other? We consider this next.

There are some parallels to be made between our psychophysical work and single-cell physiology. Truchard, Ohzawa, and Freeman (2000) explored the left- and right-eye contributions to the contrast response of binocular cells in primary visual cortex of cat. They concluded that suppressive gain control occurs initially at a purely monocular stage before linear binocular summation. This is followed by a second stage of (weaker) suppression after binocular summation (though see Macknik & Martinez-Conde, 2004). This arrangement is most similar with our two-stage model in Figure 4, although in common with other psychophysical models of binocular interactions (Blake, 1989; Cogan, 1987; Ding & Sperling, 2006; Kontsevich & Tyler, 1994; Lehky, 1988), our model also includes interocular suppression.

One of the nice properties of the twin summation model is that for binocular stimulation by masks and tests of equal size, it is identical to the Foley (1994) model, which has been fit to an extensive body of data by Foley and others. Furthermore, the number of free parameters in the twin summation model can be reduced from six to five ($p = q$) or four ($m = p$, $n = q$), with only a small drop in overall performance (see Results section) and, hence, might be preferred over the six-parameter, two-stage model on those grounds.

The two-stage model is formally different from the Foley model for the binocular case but behaves in a very similar way in most respects. However, it is unclear how the second-stage exponents should be interpreted in the two-stage model. It is possible that the entire second stage is not a seat for dynamic gain control (Heeger, 1992) but represents a static transducer. This does not violate earlier findings (e.g., Foley, 1994) because the two-stage model can accommodate dynamic gain control from a pool of mechanisms (including cross-orientation suppression) at Stage 1. In fact, as we discuss below, it is this characteristic that causes the two-stage model to be our preferred model.

Our experiments here have addressed only the situation where mask and test stimuli are spatially identical. However, a successful model of this process should generalize to the situation where the orientation or spatial frequency of the mask and test are very different. This has been investigated psychophysically by Meese and Hess (2004) who used brief stimulus durations and found different levels of suppression for superimposed monocular and dichoptic masks in a contrast-matching task. Baker and Meese (2006a, 2006b) found similar effects for contrast-masking functions at detection threshold. Both of these studies concluded that there are two routes to cross-orientation masking: an ipsiocular route excited by monoptic masks and an interocular route excited by dichoptic masks. This issue has also been addressed by single-cell work in cat (DeAngelis, Robson, Ohzawa, & Freeman, 1992; Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998; Walker, Ohzawa, & Freeman, 1998) where a similar picture has emerged. The interocular route has been attributed to cortical interactions, and the ipsiocular route has been attributed to precortical pathways (Li, Peterson, Thompson, Duong, & Freeman, 2005; Sengpiel & Vorobyov, 2005). All this prompts an important challenge for the two models. If the site of cross-orientation suppression is placed after binocular summation, as it would be for the twin summation model (see Maehara & Goryo, 2005), then cross-orientation masking must be identical for monocular and dichoptic masks. This is because the binocular site is agnostic to the eye of origin for the test. On the other hand, if cross-orientation suppression is placed before binocular summation (e.g., Stage 1 in the two-stage model), then cross-orientation weights for monocular and dichoptic suppression can be different. The psychophysical results described above (Baker & Meese, 2006a, 2006b; Meese & Hess, 2004) are inconsistent with the first arrangement but are allowed by the second (i.e., the two-stage model).

In sum, to accommodate cross-orientation masking results, the twin summation model would need to be further developed, whereas the two-stage model readily generalizes to the requirements.

What are the model equations doing?

Our experiments do not tell us why the model equations have the form that they do, and a broader context is probably needed before this becomes apparent. For example, binocular rivalry (Wilson, 2003), cross-orientation suppression (Baker & Meese, 2006a, 2006b; Foley, 1994), the correspondence problem (Banks, Gepshtein, & Landy, 2004; Fleet, Wagner, & Heeger, 1996), natural image statistics (Hibbard & Bouzit, 2006), and area summation (Meese, 2004) might all be important. In a companion paper (Baker et al., in press), we have pointed out that the two-stage model can be seen to achieve two competing demands. Above threshold, it implements weighted averaging (de Weert & Levelt, 1974) to achieve "ocularity invariance" (the invariant nature of the world whether viewed by one or two eyes). However, close to threshold, it performs almost linear summation of the signals across the two eyes, which benefits the detection of weak signals.

Conclusions

The high levels of binocular summation that we found confirm the existence of nearly linear summation of contrast across the eyes. However, careful measurement of monocular, binocular, half-binocular, and dichoptic masking functions has revealed a complexity to the functional form of early luminance contrast vision that had not previously been suspected. We have embedded this in physiologically plausible architectures containing accelerating transducers, contrast gain control, binocular summation, and late additive noise. Only the two best fitting models made good predictions for the slope of the psychometric functions. With no further fitting, these models also provided a unifying account of contrast discrimination thresholds and contrast matching between dichoptic and binocular stimuli. Features of both models are that suppression occurs within and between the eyes and that the initial monocular transduction of contrast is almost linear.

Appendix: Power-law transducers, binocular summation, and the ideal observer

We derive here the binocular/monocular sensitivity ratio that would be expected with a power-law transducer on the

contrast for each eye, followed by an ideal observer that combined independently noisy signals from the two eyes only when the stimulus input was binocular. For monocular and binocular observation,

$$d'_{mon} = c^m/\sigma, \quad d'_{bin} = 2c^m/(\sigma\sqrt{2}), \tag{A1}$$

where c is contrast, m is the transducer exponent, and σ is the standard deviation of the noise for each monocular signal. Thus, $d'_{bin} = \sqrt{2}d'_{mon}$, for any value of the exponent, m. Assuming d' is some constant k at threshold, we obtain from Equation A1 the contrast thresholds: $c_{mon} = (k\sigma)^{1/m}$ and $c_{bin} = (k\sigma\sqrt{2})^{1/m}$. Thus, the binocular advantage (threshold ratio) is $c_{mon}/c_{bin} = 2^{1/(2m)}$ irrespective of k and σ. The Weibull slope parameter $\beta \approx 1.3m$ (Pelli, 1987; Tyler & Chen, 2000) is typically around 3.5 in our data set and that of others, implying $m \approx 2.7$. Hence, the expected binocular threshold improvement for the ideal observer in this case is $c_{mon}/c_{bin} = 2^{1/5.4} = 1.14$, equivalent to 1.2 dB, compared with 4.5 dB observed in our experiments. If contrast transduction were linear ($m = 1$), then the threshold ratio predicted from this approach is $\sqrt{2}$ (3 dB), but this implies psychometric slopes β of about 1.3, far shallower than those observed at detection threshold. Thus, this analysis shows that ideal binocular combination of the noisy responses, after either linear or accelerating transduction, cannot account for the high (4.5 dB) level of binocular summation that we observed.

Acknowledgments

Commercial relationships: none.
Corresponding author: Tim S. Meese.
Email: t.s.meese@aston.ac.uk.
Address: School of Life and Health Sciences, Aston University, Birmingham, B4 7ET UK.

Footnote

[1]For most of the models, this type of matching task depends only on the mean output of the binocular summation box. Hence, only parameters prior to binocular summation can affect the behavior of the model. (In the case of the Legge-type model, this is the single parameter q.) Any nonlinearities after the binocular sum will transform the dichoptic and binocular stimuli in identical ways and, thus, cannot affect the match. The matter is slightly more complicated for the twin summation model because binocular summation takes place in parallel excitatory and suppressive pathways. For this model, matching depends on the final output after combination of the two pathways.

References

Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Visual Neuroscience, 7,* 531–546. [PubMed]

Arditi, A. R., Anderson, P. A., & Movshon, J. A. (1981). Monocular and binocular detection of moving sinusoidal gratings. *Vision Research, 21,* 329–336. [PubMed]

Baker, D. H., & Meese, T. S. (2006a). Cross-orientation suppression occurs before binocular summation: Evidence from masking and adaptation [Abstract]. *Journal of Vision, 6*(6), 821a, http://journalofvision.org/6/6/821/, doi:10.1167/6.6.821.

Baker, D. H., & Meese, T. S. (2006b). Monoptic and dichoptic cross-orientation masking are not the same mechanism [Abstract]. *Perception, 35,* 421.

Baker, D. H., Meese, T. S., & Georgeson, M. A. (2005). Contrast discrimination with simultaneous monocular and dichoptic masks [Abstract]. *Perception, 34*(Suppl.), 202.

Baker, D. H., Meese, T. S., & Georgeson, M. A. (in press). Binocular interaction: Contrast matching and contrast discrimination are predicted by the same model. *Spatial Vision.*

Banks, M. S., Gepshtein, S., & Landy, M. S. (2004). Why is spatial stereoresolution so low? *Journal of Neuroscience, 24,* 2077–2089. [PubMed] [Article]

Bird, C. M., Henning, G. B., & Wichmann, F. A. (2002). Contrast discrimination with sinusoidal gratings of different spatial frequency. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 19,* 1267–1273. [PubMed]

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review, 1,* 145–167. [PubMed]

Blake, R., & Fox, R. (1973). The psychophysical inquiry into binocular summation. *Perception & Psychophysics, 14,* 161–185.

Blake, R., & Levinson, E. (1977). Spatial properties of binocular neurons in the human visual system. *Experimental Brain Research, 27,* 221–232. [PubMed]

Blake, R., & Rush, C. (1980). Temporal properties of binocular mechanisms in the human visual system. *Experimental Brain Research, 38,* 333–340. [PubMed]

Blake, R., Sloane, M., & Fox, R. (1981). Further developments in binocular summation. *Perception & Psychophysics, 30,* 266–276. [PubMed]

Campbell, F. W., & Green, D. G. (1965). Monocular versus binocular visual acuity. *Nature, 208,* 191–192. [PubMed]

Cogan, A. I. (1987). Human binocular interaction: Towards a neural model. *Vision Research, 27,* 2125–2139. [PubMed]

DeAngelis, G. C., Robson, J. G., Ohzawa, I., & Freeman, R. D. (1992). Organization of suppression in receptive fields of neurons in cat visual cortex. *Journal of Neurophysiology, 68,* 144–163. [PubMed]

de Weert, C. M. M., & Levelt, W. J. M. (1974). Binocular brightness combinations: Additive and nonadditive aspects. *Perception and Psychophysics, 15,* 551–562.

Ding, J., & Sperling, G. (2006). A gain-control theory of binocular combination. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 1141–1146. [PubMed] [Article]

Fleet, D. J., Wagner, H., & Heeger, D. J. (1996). Neural encoding of binocular disparity: Energy models, position shifts and phase shifts. *Vision Research, 36,* 1839–1857. [PubMed]

Foley, J. M. (1994). Human luminance pattern-vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 11,* 1710–1719. [PubMed]

Foley, J. M., & Chen, C. C. (1999). Pattern detection in the presence of maskers that differ in spatial phase and temporal offset: Threshold measurements and a model. *Vision Research, 39,* 3855–3872. [PubMed]

Foley, J. M., & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research, 21,* 1041–1053. [PubMed]

Georgeson, M. A., & Meese, T. S. (2004). Contrast discrimination and pattern masking: Contrast gain control with fixed additive noise [Abstract]. *Perception, 33,* 754–755.

Georgeson, M. A., & Meese, T. S. (2005). Binocular summation at contrast threshold: A new look. *Perception, 34*(Suppl.), 138.

Georgeson, M. A., & Meese, T. S. (2006). Fixed or variable noise in contrast discrimination? The jury's still out…. *Vision Research, 46,* 4294–4303. [PubMed]

Georgeson, M. A., Meese, T. S., & Baker, D. H. (2005). Binocular summation, dichoptic masking and contrast gain control [Abstract]. *Journal of Vision, 5*(8), 797a, http://journalofvision.org/5/8/797/, doi:10.1167/5.8.797.

Graham, N. (1989). *Visual pattern analyzers*. Oxford: Oxford University Press.

Green, M., & Blake, R. (1981). Phase effects in monoptic and dichoptic temporal integration: Flicker and motion detection. *Vision Research, 21,* 365–372. [PubMed]

Harrad, R. A., & Hess, R. F. (1992). Binocular integration of contrast information in amblyopia. *Vision Research, 32,* 2135–2150. [PubMed]

Harris, J. M., & Willis, A. (2001). A binocular site for contrast-modulated masking. *Vision Research, 41,* 873–881. [PubMed]

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience, 9,* 181–197. [PubMed]

Hibbard, P. B., & Bouzit, S. (2006). Binocular energy responses to natural images [Abstract]. *Journal of Vision, 6*(6), 833a, http://journalofvision.org/6/6/833/, doi:10.1167/6.6.833.

Holmes, D. J., & Meese, T. S. (2004). Grating and plaid masks indicate linear summation in a contrast gain pool. *Journal of Vision, 4*(12), 1080–1089, http://journalofvision.org/4/12/7/, doi:10.1167/4.12.7. [PubMed] [Article]

Katkov, M., Gan, T., Tsodyks, M., & Sagi, D. (2005). Singularities in the inverse modeling of contrast discrimination and ways to avoid them [Abstract]. *Journal of Vision, 5*(8), 455a, doi:10.1167/5.8.455, http://journalofvision. org/5/8/455/.

Katkov, M., Tsodyks, M., & Sagi, D. (2006). Singularities in the inverse modeling of 2AFC contrast discrimination data. *Vision Research, 46,* 259–266. [PubMed]

Kontsevich, L. L., Chen, C. C., & Tyler, C. W. (2002). Separating the effects of response nonlinearity and internal noise psychophysically. *Vision Research, 42,* 1771–1784. [PubMed]

Kontsevich, L. L., & Tyler, C. W. (1994). Analysis of stereothresholds for stimuli below 2.5 c/deg. *Vision Research, 17,* 2317–2329. [PubMed]

Kontsevich, L. L., & Tyler, C. W. (1999). Nonlinearities of near-threshold contrast transduction. *Vision Research, 39,* 1869–1880. [PubMed]

Lasley, D. J., & Cohn, T. E. (1981). Why luminance discrimination may be better than detection. *Vision Research, 21,* 273–278. [PubMed]

Legge, G. E. (1979). Spatial frequency masking in human vision: Binocular interactions. *Journal of the Optical Society of America, 69,* 838–847. [PubMed]

Legge, G. E. (1984a). Binocular contrast summation—I. Detection and discrimination. *Vision Research, 24,* 373–383. [PubMed]

Legge, G. E. (1984b). Binocular contrast summation—II. Quadratic summation. *Vision Research, 24,* 385–394. [PubMed]

Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America, 70,* 1458–1471. [PubMed]

Legge, G. E., Kersten, D., & Burgess, A. E. (1987). Contrast discrimination in noise. *Journal of the Optical Society of America A, Optics and Image Science, 4,* 391–404. [PubMed]

Legge, G. E., & Rubin, G. S. (1981). Binocular interactions in suprathreshold contrast perception. *Perception & Psychophysics, 30,* 49–61. [PubMed]

Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception, 17,* 215–228. [PubMed]

Lema, S. A., & Blake, R. (1977). Binocular summation in normal and stereoblind humans. *Vision Research, 17,* 691–695. [PubMed]

Leonards, U., & Sireteanu, R. (1993). Interocular suppression in normal and amblyopic subjects: The effect of unilateral attenuation with neutral density filters. *Perception & Psychophysics, 54,* 65–74. [PubMed]

Levi, D. M. (1985). Binocular interactions and their alterations resulting from abnormal visual experience. In D. Rose & V. G. Dobson (Eds.), *Models of the visual cortex* (pp. 200–210). New York: Wiley.

Levi, D. M., Harwerth, R. S., & Smith, E. L., III. (1979). Humans deprived of normal binocular vision have binocular interactions tuned to size and orientation. *Science, 206,* 852–854. [PubMed]

Li, B., Peterson, M. R., Thompson, J. K., Duong, T., & Freeman, R. D. (2005). Cross-orientation suppression: monoptic and dichoptic mechanisms are different. *Journal of Neurophysiology, 94,* 1645–1650. [PubMed] [Article]

Macknik, S. L., & Martinez-Conde, S. (2004). Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: Implications for binocular vision and visual awareness. *Journal of Cognitive Neuroscience, 16,* 1049–1059. [PubMed]

Maehara, G., & Goryo, K. (2005). Binocular, monocular and dichoptic pattern masking. *Optical Review, 12,* 76–82.

McIlhagga, W. (2004). Denoising and contrast constancy. *Vision Research, 44,* 2659–2666. [PubMed]

McKee, S. P., Bravo, M. J., Taylor, D. G., & Legge, G. E. (1994). Stereo matching precedes dichoptic masking. *Vision Research, 34,* 1047–1060. [PubMed]

Meese, T. S. (2004). Area summation and masking. *Journal of Vision, 4*(10), 930–943, http://journalofvision.org/4/10/8/, doi:10.1167/4.10.8 [PubMed] [Article]

Meese, T. S., Georgeson, M. A., & Baker, D. H. (2005). Interocular masking and summation indicate two stages of divisive contrast gain control [Abstract]. *Perception, 34*(Suppl.), 42–43.

Meese, T. S., Georgeson, M. A., & Hess, R. F. (2004). Binocular summation, interocular suppression and contrast gain control: Psychophysical model and data [Abstract]. *Perception, 33*(Suppl.), 41.

Meese, T. S., & Hess, R. F. (2004). Low spatial frequencies are suppressively masked across spatial scale, orientation, field position, and eye of origin. *Journal of Vision, 4*(10), 843–859, http://journalofvision.org/4/10/2/, doi:10.1167/4.10.2. [PubMed] [Article]

Meese, T. S., & Hess, R. F. (2005). Interocular suppression is gated by interocular feature matching. *Vision Research, 45,* 9–15. [PubMed]

Meese, T. S., Hess, R. F., & Williams, C. B. (2001). Spatial coherence does not affect contrast discrimination for multiple Gabor stimuli. *Perception, 30,* 1411–1422. [PubMed]

Meese, T. S., Hess, R. F., & Williams, C. B. (2005). Size matters, but not for everyone: Individual differences for contrast discrimination. *Journal of Vision, 5*(11), 928–947, http://journalofvision.org/5/11/2/, doi:10.1167/5.11.2. [PubMed] [Article]

Nachmias, J. (1981). On the psychometric function for contrast detection. *Vision Research, 21,* 215–223. [PubMed]

Nachmias, J., & Sansbury, R. V. (1974). Grating contrast: Discrimination may be better than detection. *Vision Research, 14,* 1039–1042. [PubMed]

Pardhan, S., & Gilchrist, J. (1992). Binocular contrast summation and inhibition in amblyopia. The influence of the interocular difference on binocular contrast sensitivity. *Documenta Ophthalmologica, 82,* 239–248. [PubMed]

Pardhan, S., & Whitaker, A. (2003). Binocular summation to gratings in the peripheral field in older subjects is spatial frequency dependent. *Current Eye Research, 26,* 297–302. [PubMed]

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 1508–1532. [PubMed]

Pelli, D. G. (1987). On the relation between summation and facilitation. *Vision Research, 27,* 119–123. [PubMed]

Petrov, Y., & McKee, S. P. (2006). The effect of spatial configuration on surround suppression. *Journal of Vision, 6*(3), 224–238, http://journalofvision.org/6/3/4/, doi:10.1167/6.3.4. [PubMed] [Article]

Petrov, Y., Verghese, P., & McKee, S. P. (2006). Collinear facilitation is largely uncertainty reduction. *Journal of Vision, 6*(2), 170–178, http://journalofvision.org/6/2/8/, doi:10.1167/6.2.8. [PubMed] [Article]

Quick, R. F., Jr. (1974). A vector-magnitude model of contrast detection. *Kybernetik, 16,* 65–67. [PubMed]

Rose, D. (1978). Monocular versus binocular contrast thresholds for movement and pattern. *Perception, 7,* 195–200. [PubMed]

Rose, D. (1980). The binocular: Monocular sensitivity ratio for movement detection varies with temporal frequency. *Perception, 9,* 577–580. [PubMed]

Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society B: Biological Sciences, 246,* 61–69. [PubMed] [Article]

Sengpiel, F., Baddeley, R. J., Freeman, T. C., Harrad, R., & Blakemore, C. (1998). Different mechanisms underlie three inhibitory phenomena in cat area 17. *Vision Research, 38,* 2067–2080. [PubMed]

Sengpiel, F., & Vorobyov, V. (2005). Intracortical origins of interocular suppression in the visual cortex. *The Journal of Neuroscience, 25,* 6394–6400. [PubMed] [Article]

Simmons, D. R. (2005). The binocular combination of chromatic contrast. *Perception, 34,* 1035–1042. [PubMed]

Smith, E. L., III, Chino, Y., Ni, J., & Cheng, H. (1997). Binocular combination of contrast signals by striate cortical neurons in the monkey. *Journal of Neurophysiology, 78,* 366–382. [PubMed] [Article]

Snowden, R. J., & Hammett, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast, and contrast discrimination. *Vision Research, 38,* 1935–1945. [PubMed]

Strasburger, H. (2001). Invariance of the psychometric function for character recognition across the visual field. *Perception & Psychophysics, 63,* 1356–1376. [PubMed] [Article]

Stromeyer, C. F., III, & Klein, S. (1974). Spatial frequency channels in human vision as asymmetric (edge) mechanisms. *Vision Research, 14,* 1409–1420. [PubMed]

Tolhurst, D. J., & Heeger, D. J. (1997). Comparison of contrast-normalization and threshold models of the responses of simple cells in cat striate cortex. *Visual Neuroscience, 14,* 293–309. [PubMed]

Truchard, A. M., Ohzawa, I., & Freeman, R. D. (2000). Contrast gain control in the visual cortex: Monocular versus binocular mechanisms. *The Journal of Neuroscience, 20,* 3017–3032. [PubMed] [Article]

Tyler, C. W., & Chen, C. C. (2000). Signal detection theory in the 2AFC paradigm: Attention, channel uncertainty and probability summation. *Vision Research, 40,* 3121–3144. [PubMed]

Tyler, C. W., & Kontsevich, L. L. (2005). The structure of stereoscopic masking: Position, disparity, and size tuning. *Vision Research, 45,* 3096–3108. [PubMed]

Valberg, A., & Fosse, P. (2002). Binocular contrast inhibition in subjects with age-related macular degeneration. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 19,* 223–228. [PubMed]

Walker, G. A., Ohzawa, I., & Freeman, R. D. (1998). Binocular cross-orientation suppression in the cat's striate cortex. *Journal of Neurophysiology, 79,* 227–239. [PubMed] [Article]

Webb, B. S., Tinsley, C. J., Barraclough, N. E., Parker, A., & Derrington, A. M. (2003). Gain control from beyond the classical receptive field in primate primary visual cortex, *Visual Neuroscience, 20,* 221–230. [PubMed]

Westendorf, D. H. (1989). Binocular rivalry and dichoptic masking: Suppressed stimuli do not mask stimuli in a dominating eye. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 485–492. [PubMed]

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling and goodness of fit. *Perception & Psychophysics, 63,* 1293–1313. [PubMed] [Article]

Wilson, H. R. (1980). A transducer function for threshold and suprathreshold human vision. *Biological Cybernetics, 38,* 171–178. [PubMed]

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America, 100,* 14499–14503. [PubMed] [Article]

Yang, J., & Makous, W. (1995). Modelling pedestal experiments with amplitude instead of contrast. *Vision Research, 35,* 1979–1989. [PubMed]