

## BINOCULAR COMBINATION OF CONTRAST SIGNALS

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**Abstract**—We studied the detectability of dichoptically presented vertical grating patterns that varied in the ratio of the contrasts presented to the two eyes. The resulting threshold data fall on a *binocular summation contour* well described by a power summation equation with an exponent near 2. We studied the effect of adding one-dimensional visual noise, either correlated or uncorrelated between the eyes, to the grating patterns. The addition of uncorrelated noise elevated thresholds uniformly for all interocular ratios, while correlated noise elevated thresholds for stimuli whose ratios were near 1 more than thresholds for other stimuli. We also examined the effects of monocular adaptation to a high-contrast grating on the form of the summation contour. Such adaptation elevates threshold in a manner that varies continuously with the interocular contrast ratio of the test targets, and increases the amount of binocular summation. Each of several current models can explain some of our results, but no one of them seems capable of accounting for all three sets of data. We therefore develop a new multiple-channel model, the *distribution model*, which postulates a family of linear binocular channels that vary in their sensitivities to the two monocular inputs. This model can account for our data and those of others concerning binocular summation, masking, adaptation and interocular transfer. We conclude that there exists a system of *ocular dominance channels* in the human visual system.

Binocular summation    Contrast detection    Interocular transfer

### INTRODUCTION

Visual targets are better detected with two eyes than one. This *binocular summation*† is often cited as evidence that inputs from the two eyes interact prior to the decision concerning detection (see Blake & Fox, 1973; Blake, Sloane & Fox, 1981). The simplest interaction that might account for binocular summation is the probabilistic combination of signals from two independent monocular channels, but when identical stimuli are presented to the two eyes, binocular summation is greater than predicted by probability summation (Eriksen, 1966; Green & Swets, 1966; Westendorf & Fox, 1975; Arditi, Anderson & Movshon, 1981; Legge, 1984a). Binocular summation also exceeds empirical estimates of probability summation (e.g. Matin, 1962; Erikson & Greenspon, 1968; Thorn & Boynton, 1974). Some more direct

combination of monocular signals thus appears to be involved.

Several attempts have been made to model a neural summation process. Campbell and Green (1965) proposed that a single binocular channel could account for binocular and monocular grating detection. They measured monocular and binocular contrast sensitivities for stationary sinusoidal gratings and found that the ratio of binocular to monocular sensitivity was consistently near  $\sqrt{2}$  (see also Blake & Levinson, 1977; Arditi et al., 1981b). Campbell and Green proposed that the monocular signals are algebraically summed prior to detection, but that noise, uncorrelated between the eyes, is added to the signals peripherally. When two independent samples of this noisy process are summed, the signal is doubled but the standard deviation of the noise increases only by a factor of  $\sqrt{2}$ . Assuming that detection is based on a signal-to-noise discrimination, an observer should be able to detect a contrast using both eyes that is  $\sqrt{2}$  lower than can be detected using one eye. There is, however, a subtle problem with Campbell and Green's model. If the added noise is of *peripheral* origin, then the observer must be able to identify and discount noise arising from one

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†The term "binocular summation" is misleading, since it implies that monocular signals are literally summed. We use the term in a descriptive sense to mean some form of combination of binocular signals prior to detection.

eye when the signal is presented to the other—otherwise the  $\sqrt{2}$  improvement would not be seen binocularly. But normal observers have difficulty in identifying the eye of origin of visual signals (e.g. Blake & Cormack, 1979), and it is difficult to see how they could identify the eye of origin of the noise limiting performance.

More recently, Legge (1984b) has proposed a quadratic summation model that also predicts a  $\sqrt{2}$  ratio of binocular to monocular contrast sensitivity. In Legge's model, a square-law non-linearity operates on the monocular signals to yield a measurement related to signal energy; the energy signals from the two eyes are summed and then passed through a compressive nonlinearity. Legge's model overcomes some of the difficulties in Campbell and Green's formulation, but resembles the earlier model in that perceptual decisions are based on the output of a single mechanism that sums transformed representations of monocular signals.

The substrate for binocular summation is commonly assumed to be binocular neurons analogous to those found in cat and monkey visual cortex (Hubel & Wiesel, 1962, 1968). Visual cortical neurons differ in the extent to which they can be activated by stimulation of the two eyes, that is, in their *ocular dominance*. Some neurons appear monocular, being activated exclusively by stimulation of the right or left eye alone. The majority are binocular, but vary in the relative effectiveness of the two eyes in causing excitation. The optimal stimulus for a binocular neuron is invariably very similar in the two eyes (e.g. Hubel & Wiesel, 1962, 1968; Blakemore, Fiorentini & Maffei, 1972; Nelson, Kato & Bishop, 1977). This suggests that similar binocular neurons in humans might provide the substrate for binocular summation, since summation is greatest when the monocular stimuli move in the same direction, are similar in spatial and temporal character, and stimulate corresponding retinal areas (Matin, 1962; Westendorf & Fox, 1975; Bacon, 1976; Arditi et al.,

1981; Blake & Levinson, 1977; Green & Blake, 1981; Legge, 1984a, 1984b).

The primary visual cortex is also thought to be the site at which spatial adaptation effects occur. Following monocular adaptation to a grating, the threshold contrast for detection of a similar grating is elevated in the unadapted eye, suggesting the involvement of binocular mechanisms, or neurons (e.g. Blakemore & Campbell, 1969). The aftereffect is typically larger in the adapted eye than in the unadapted eye, which may imply the involvement of monocular neurons (Blake, Overton & Lema-Stern, 1981; Sloane & Blake, 1984). A central issue, to which we return in the Discussion, is whether neurons that differ in their ocular dominance properties provide the substrate for more than one detection *channel*. The distribution of ocular dominance across visual cortical neurons is apparently continuous, and might therefore provide the substrate for many detection channels, so long as signals from each collection of neural *mechanisms* of a particular ocular dominance can be used separately to support perceptual judgements. If, on the other hand, signals from many mechanisms of different ocular dominance are pooled or averaged, the information is collapsed into a single *channel\** (Anderson, Mitchell & Timney, 1980; Blake et al., 1981a).

The experiments reported here were undertaken to determine whether a single-channel model like those proposed by Campbell and Green and by Legge can account for the phenomena of binocular summation and interocular transfer, or whether a more complex model is needed. Our data are inconsistent with current models having a single binocular channel, but conform to a new model based on physiological and psychophysical data suggesting the existence of multiple binocular channels that vary along the dimension of ocular dominance.

We have briefly reported some of these results elsewhere (Anderson & Movshon, 1981), and they formed a portion of a Ph.D. dissertation (Anderson, 1982).

## METHODS

### *Apparatus and stimuli*

Stimuli were generated by a PDP11 computer on two Tektronix display oscilloscopes with matched P31 phosphors, using conventional television techniques. The frame rate of the display was 64 Hz. The two CRT screens subtended 5 by 6 deg at the viewing distance of

\*The term "binocular mechanism" typically refers to a site in the visual pathway where signals from the two eyes are combined, matched or compared; "monocular mechanism" refers to a stage of visual processing where the independence of signals from each eye is preserved. In this paper, when the term "mechanism" is replaced by "channel", we imply reference *both* to a stage of visual processing *and* to an associated detection device. Models can thus be distinguished as being composed of a single or of multiple channels; a single channel can be composed of single or multiple mechanisms.

114 cm, and were viewed (using a conventional Wheatstone stereoscope arrangement) through rectangular holes in a large opalescent screen 30 cm from the observer. This screen was back-illuminated so as to closely match the oscilloscope faces in hue and intensity; the borders of the apertures in this screen were defocused to a degree that provided a gradual transition from CRT screen to surround. The space- and time-average luminance of each display was constant at a value between 3 and 25 cd/m<sup>2</sup>; for each experimental series, the luminance of the two displays was identical. The room was dark except for ambient illumination provided by the stimulus display. Observers viewed the display through natural pupils, using their normal optical correction if required. Head position was stabilized through the use of a chin rest. Small, black fixation circles and Nonius lines were placed in the center of each screen to aid in establishing and monitoring binocular alignment. Observers were instructed to make sure that the Nonius lines always appeared vertically aligned before making any perceptual judgement.

In all experiments, vertical sinusoidal gratings were used as stimuli. The contrasts of the gratings presented on the two screens were controlled by two programmable 9-bit logarithmic attenuators, providing between 0 and 95.75 dB of attenuation in 0.25 dB steps; low-level noise in the system precluded the use of attenuations in excess of 75 dB.

We also used dynamic one-dimensional visual noise, which consisted of random fluctuations in luminance in time and space along a horizontal axis. This stimulus appears as a pattern of vertical stripes of varying width rapidly changing in position. The outputs of two noise generators (Grason-Stadler, models 901 and 901B) provided the band-limited visual noise. The noise spectral density was uniform up to about 4 c/deg and fell thereafter at 6 dB/octave. Computer-controlled electronic switches made it possible for the noise signals applied to the Z-axes of the two oscilloscopes to come from the same noise generator or from different noise generators. The root-mean-square (r.m.s.) contrast of the noise was controlled by analog multiplication of the noise signal by a voltage value provided by a 12-bit digital-to-analog converter. When both oscilloscopes received a noise signal from the same noise generator, the noise on the two oscilloscope screens was the same (i.e. perfectly correlated and at zero

disparity). When the two displays received noise signals from independent sources, they contained uncorrelated noise of equal r.m.s. contrast. The rasters on both oscilloscopes were produced by the same function generator. This, in combination with careful calibrations of gain and geometry, ensured that correlated signals on the two screens were in perfect spatial register at all times.

Following multiplication, the noise signals were applied to the Z-axes of the oscilloscopes. Since the noise was presented as a series of uncorrelated frames, the luminance of any line on the screen varied as Gaussian white noise sampled at a rate of 64 Hz.

Threshold contrasts were obtained for 9 grating stimuli. This stimulus set consisted of two monocularly-presented gratings and seven binocularly-presented gratings; the monocular components of the binocular stimuli were identical in all respects save contrast. The binocular gratings had interocular contrast ratios (both left-to-right eye and right-to-left eye) of 1:1, 1:1.4, 1:2 and 1:4. In determining the threshold contrast for a particular stimulus, the contrasts of the left and right eye's components of the stimuli were covaried so that the ratio of the two monocular components remained fixed. For the basic binocular summation experiment and for the adaptation experiment, we measured contrast thresholds for gratings of a range of moderate spatial frequencies (1.5–6 c/deg). The contrast of the stimuli was either sinusoidally modulated at 4 Hz, turned on and off once per second, or received no temporal modulation. Neither the spatial frequency nor the nature of the temporal modulation had any consistent effect on the results. In the noise masking experiments, the gratings had a spatial frequency of 1.5 c/deg, well within the spatial bandpass of the noise. When stimuli were presented monocularly, the opposite eye viewed a uniform field of the same mean luminance as the stimulus.

#### *Psychophysical procedure*

Threshold contrasts were obtained using two psychophysical methods: the method of adjustment and a staircase method. For the staircase method, data were collected using a two interval forced choice (2IFC) procedure.

*Method of adjustment.* The observer adjusted the contrast of a stimulus to the desired level by means of a ten-turn potentiometer, whose value was read by an analog-to-digital converter.

When the desired setting was made, the observer pressed a button; releasing the button initiated the presentation of the next stimulus. After each adjustment trial, the relationship between the position of the potentiometer and stimulus contrast was randomly altered so that the subject had no positional cue to contrast. From 9 to 20 stimuli were presented 9 times each in a single session. In each of 8 blocks of trials, the order of the stimuli was randomly shuffled and each was presented once. Data from all blocks of trials were collected and the antilog of the mean of the adjusted attenuation settings (in logarithmic units) was taken as the estimate of the threshold contrast for a stimulus. When the method of adjustment was used in the noise masking experiments, the noise and grating were continuously present on each trial and the grating's contrast was sinusoidally modulated at 4 Hz. In all experiments, the standard error of the mean of 8 data points rarely exceeded 0.05 log unit (1 dB) and was typically about 0.025 log unit (0.5 dB). Adjustment sessions were 15–20 min in duration.

The method of adjustment was modified for use in the adaptation experiments. At the beginning of a session, observers fixated the center of the display and inspected a grating of 40% contrast, which was seen by only one eye. The contrast of this grating was square wave-modulated at 1 Hz in order to prevent the formation of an afterimage; the other eye viewed a homogeneous field of the same luminance as the grating. Following a 60 sec initial period of adaptation, a test stimulus appeared and the observer adjusted its contrast to threshold. The settings were typically made in 2–4 sec. When the observer had made a setting, he received an 8 sec topping-up presentation of the adapting grating. These 8 sec exposures, which were sufficient to keep the adaptation effect at its maximum, alternated with presentations of the test stimuli. The adapting and test gratings were identical in spatial frequency and orientation.

*Staircase method.* In some of the noise masking experiments, the contrast of the gratings was varied according to one of the transformed staircase methods described by Levitt (1970). Stimulus contrast was decreased if three consecutive correct responses were made and increased if one incorrect response was made. This staircase rule causes the contrast value to approach that required for correct detection on 79% of the trials. An experimental session consisted of several interleaved staircases. The step size for

each staircase was initially set to be 6 dB; the step size was halved logarithmically after each reversal until it reached its final size of 1 dB. Each staircase was normally run for a total of 80–100 trials, resulting in an average of 18 reversals per staircase. The levels visited after the fifth reversal were averaged to give the estimate of threshold contrast. Staircase sessions were roughly 45 min in length.

For the staircase procedure, a balanced 2IFC design was used. On each trial, tone bursts marked the occurrence of two temporal intervals, each 500 msec in duration separated by 200 msec. One interval, chosen at random, contained the grating stimulus, which was presented for 125 msec in the center of the interval. If a visual noise mask was involved, the noise was present throughout the 500 msec of each interval. The onset and offset of both signal and noise was abrupt. Observers chose the interval in which the grating stimulus was presented by pressing one of two buttons; the response initiated the next trial. Auditory feedback was provided after each trial.

#### *Observers*

Eight observers participated in some or all of the experiments reported here. All had normal or corrected-to-normal visual acuity and good stereopsis. Four of the observers (J.K., E.A., M.G. and M.P.) were totally or partially naive as to the purposes of the study. The remaining four (P.A., J.A.M., G.I. and R.S.) were aware of the aims of the experiments. The use of forced choice techniques and the difficulty experienced by all observers in identifying the eye-of-origin of monocular stimuli or in discriminating monocular from binocular stimuli (Blake & Cormack, 1979) prevented their knowledge from influencing the results.

## RESULTS

### *The binocular summation contour*

Typically, studies of binocular summation compare sensitivities for monocularly and binocularly viewed stimuli. We extended this paradigm by measuring threshold contrasts for gratings that varied in the *ratio* of contrasts presented to the two eyes. The method is analogous to that used to study the detectability of compound gratings by Graham and Nachmias (1971). For each observer, we measured threshold contrasts for 9 stimuli of differing interocular contrast ratio at one or more spatial



frequencies. The data describe a *binocular summation contour*. Figure 1A shows one set of data for observer E.A.; the spatial frequency of the gratings, which were stationary, was 2.6 c/deg. The abscissa gives the contrast of the left eye's component of the stimuli at threshold; the ordinate gives the threshold contrast for the right eye's component. Since the ratio of the two monocular components of a stimulus remained fixed, adjusting the contrast of a stimulus moved its representation in this plot along a radius passing through the origin. The dashed lines

indicate two extreme types of binocular combination; the diagonal dashed line shows the prediction of a perfect linear summation model and the dashed lines forming the upper and right edges of the square represent the prediction of a model of perfect independence between the eyes (with no probability summation). The binocular summation contour data lie between these two cases.

We fit binocular summation contours with a three-parameter power summation equation:

$$(m_l/\alpha_l)^\sigma + (m_r/\alpha_r)^\sigma = 1; \quad (1)$$

where  $m_l$  and  $m_r$  are the contrasts for the left and right eye components of stimuli at threshold, the parameters  $\alpha_l$  and  $\alpha_r$  are the independently-measured monocular threshold contrasts, and the exponent  $\sigma$  is a parameter inversely related to the amount of summation (see Watson, Thompson, Murphy & Nachmias, 1980). The normalization using  $\alpha_r$  and  $\alpha_l$  is based on the assumption that any sensitivity disparity between the eyes is accounted for by a simple multiplicative scaling. When  $\sigma$  is 2, this equation represents the prediction of Legge's quadratic summation model (1984b).

To fit equation 1 to the data, we minimized the statistic  $X^2$ , using the STEPIT routine of Chandler (1965). The statistic, described in Appendix I, takes into account the variance associated with each data point in determining a fit. In Fig. 1B the normalized threshold contrasts presented in Fig. 1A are fit to equation 1. The value of  $\sigma$  is 2.0. Note that when  $\sigma = 2$  and  $\alpha_l = \alpha_r$ , the ratio of binocular to monocular contrast sensitivity is the ubiquitous  $\sqrt{2}$ . For this observer, the monocular threshold contrasts were almost identical in the two eyes ( $\alpha_l = 0.0094$ ,  $\alpha_r = 0.0092$ ). The normalization can be removed to produce a plot with contrast on the two axes, the format used for subsequent figures. If  $\alpha_l = \alpha_r$ , then the shapes of the normalized and nonnormalized contours are the same.

Data for two other observers are shown in Fig. 2. Observer M.G. (Fig. 2A) viewed gratings of 2.6 c/deg flashed on for 500 msec each second. These data fit equation 1 with a  $\sigma$  of 1.4, representing a binocular-to-monocular contrast sensitivity ratio of 1.6. The stimuli viewed by observer J.A.M. (Fig. 2B) were stationary gratings of 5 c/deg. The data are fit by a  $\sigma$  of 2.9, representing a binocular-to-monocular sensitivity ratio of 1.25. The 20  $\sigma$  values obtained across all observers and conditions have a mean of 2.18 (SD = 0.73), and range from 1.4 to 4.6. 15 of the

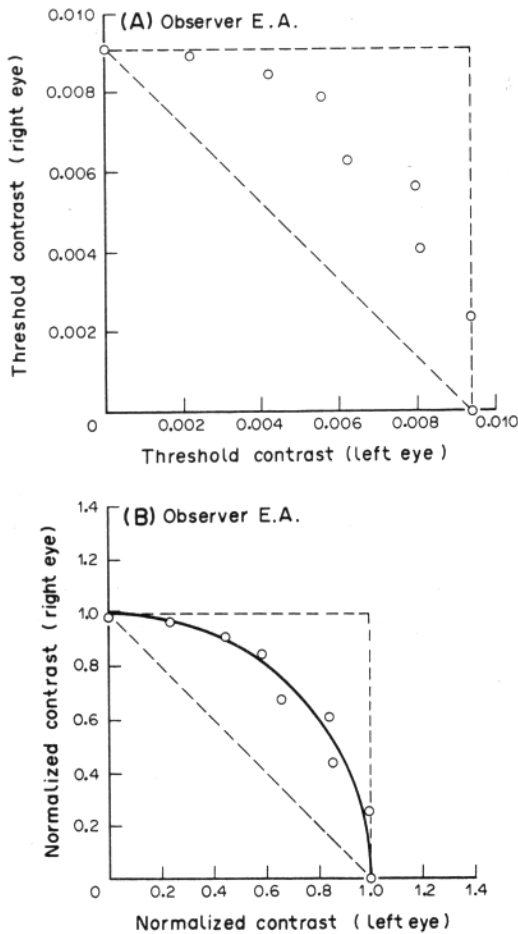


Fig. 1. Binocular summation data for one observer. (A) The abscissa gives the threshold contrast of the left eye's component of the stimulus; the ordinate shows the threshold contrast for the right eye's component. Each datum represents the mean of 8 settings made by the modified method of adjustment described in the text. The dashed lines indicate two extreme forms of binocular combination—linear summation and perfect independence between the eyes. See text for details. (B) The same data are replotted, fit to equation 1. The abscissa gives the contrast of the left eye's component of the stimuli normalized with respect to the monocular contrast for the left eye alone. The ordinate shows the normalized threshold contrast for the right eye's component. The value of the summation parameter  $\sigma$  for this set of data is 2.0.

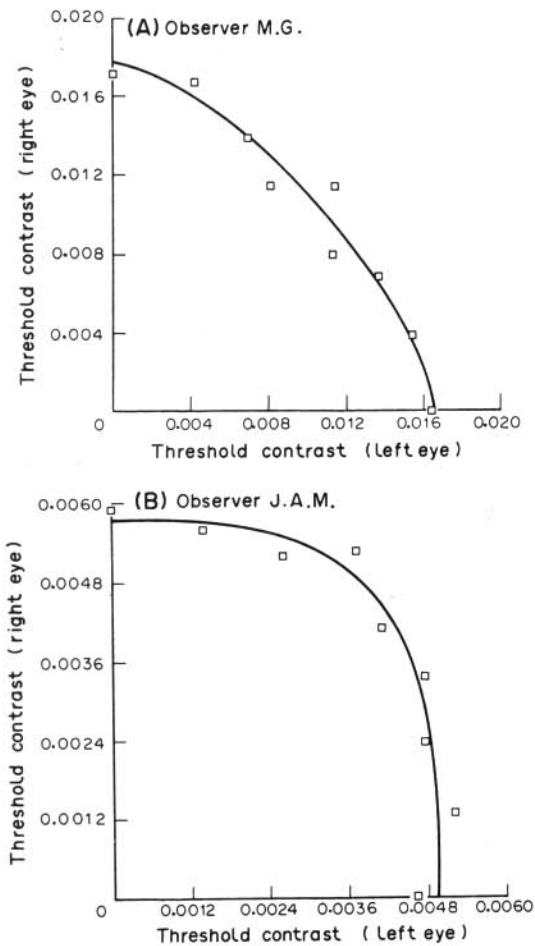


Fig. 2. Binocular summation data for two observers fit by equation 1. Here and hereafter, unnormalized physical contrast is plotted on the axes, resulting in curves whose symmetry is related to a sensitivity difference between the eyes. The value of the exponent  $\sigma$  for M.G. (A) is 1.4 and for J.A.M. (B) it is 2.9.

20 values fall between 1.5 and 2.5. Generally, equation 1 provided a good fit to most of the binocular summation contours. For 14 of 20 data sets, the value of the  $X^2$  statistic for goodness of fit (Appendix I) was below 12.6, the critical value for rejection of the fit at a confidence level of 0.05 (range: 0.4–10.9). Most of the values of  $X^2$  which exceeded this critical value did so by a small amount (range: 13.4–17.3), corresponding to confidence levels as low as about 0.025. Moreover, the goodness of the fit was not consistently related to such other factors as spatial frequency, the degree of binocular summation, or the identity of the observer. Thus we believe that the few marginal values do not form strong grounds for rejection of the fit.

Legge's (1984b) model predicts binocular summation contours having the form given by

equation 1, but with  $\sigma$  equal to 2. To examine this prediction, we fit the same 20 data sets again with the constraint that  $\sigma = 2$ . Only two of the 14 data sets fit acceptably by a free varying value of  $\sigma$  could not be acceptably fit by a  $\sigma$  of 2; not surprisingly, these two cases were fit with  $\sigma$  values at the extremes of the range. Of the 8 data sets that exceeded the critical rejection value (now 14.1 because of the change in the degrees of freedom), only 2 had extreme values greater than 20. It is therefore reasonable to conclude that a power summation law with an exponent of 2 adequately describes the bulk of our data.

*Experimental alteration of binocular summation.* Our strategy for comparing single- and multiple-channel models of binocular summation was to establish whether the form of the binocular summation contour could be altered experimentally. If the contour is determined by the summation characteristics of a single channel, then its shape should be *invariant* across conditions. If, on the other hand, the contour represents the combined action of several channels whose behavior can be independently manipulated, it should be possible to alter its shape. We used both masking and adaptation procedures to attempt to alter the shape of the contour. Our reasoning is thus formally equivalent to that used by Blakemore and Campbell (1969) and Stromeyer and Julesz (1972) in their studies of the effects of adaptation and masking on the shape of the spatial modulation transfer function.

*Effects of visual noise on binocular summation.* The first set of experiments concerned the effect of the interocular correlation between fields of masking noise on the form of the binocular summation contour. We used dynamic random one-dimensional noise that was either identical (correlated) or independent (uncorrelated) in the two eyes; in either case the r.m.s. contrast and spectral energy density of each eye's noise were identical. Interpretation of our results required that we verify that the detectability of gratings in dynamic visual noise is determined by the signal-to-noise ratio at some central site. Studies of masking by *dynamic* visual noise typically report the threshold contrast for a grating to be proportional to noise contrast above some threshold value (e.g. Stromeyer & Julesz, 1972; Pelli, 1981). When *static* noise is used, this relationship does not always obtain (Arend & Smith, 1982; see also Braccini, Gambardella & Suetta, 1980), perhaps because

observers familiarize themselves with the characteristics of each sample of noise.

To determine if threshold contrast for a grating was proportional to noise contrast under our conditions, and to determine a suitable masking contrast, we presented observers with four masked detection conditions: a monocular grating with a monocular noise mask, for each eye; a binocular grating (identical contrast to each eye) with binocular correlated noise; and a binocular grating (same contrast to both eyes) with binocular uncorrelated noise. In each condition, we determined detection thresholds for the grating alone and for the grating masked by several different noise contrasts. Because the masking noise was dynamic, we used a test target modulated at the moderate temporal frequency of 4 Hz. The stimuli for all test and masking conditions were intermixed during a session. Adjustment and staircase methods gave very similar results, and the results for different observers were remarkably consistent.

Data collected by the method of adjustment for observer J.K. are shown in Fig. 3. The coordinates give threshold contrast for a grating as a function of the r.m.s. contrast of the noise per eye. The dashed diagonal has unit slope. When noise contrast was zero, the threshold contrast for the grating alone is plotted. As external noise contrast increases, the functions are initially flat—the added noise did not influence detection. At a noise contrast near 0.01

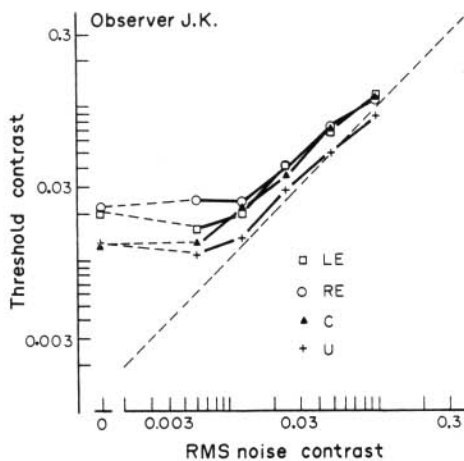


Fig. 3. Contrast thresholds for gratings as a function of the r.m.s. contrast of the noise mask, for observer J.K. Data points are the means of 8 adjustment settings. The different symbols show data for four different stimulus conditions: LE = monocular left eye grating - monocular left eye noise; RE = monocular right eye grating - monocular right eye noise; C = binocular grating - binocular correlated noise; and U = binocular grating - binocular uncorrelated noise. The dashed diagonal line has a slope of 1.0.

(roughly the r.m.s. contrast at which the noise became visible), threshold contrast began to rise with a slope near unity. This behavior has been described by Stromeyer and Julesz (1972) and Pelli (1981). The usual interpretation is that threshold is determined by a signal-to-noise ratio in which the noise has two components, one internal and one external, which add. At low noise contrasts, internal noise dominates performance and threshold is uniform. At high contrasts, external noise dominates internal noise, and threshold is proportional to noise contrast. Above the "knee" of the function, threshold depends *only* on the ratio of signal to external noise.

In the absence of added noise, monocular and binocular thresholds differed by approximately a factor of  $\sqrt{2}$ . As the noise contrast was increased, the thresholds for all targets began to rise. Although the effect is relatively subtle in Fig. 3, the threshold for binocular gratings in binocular noise (C) begins to rise at a slightly lower noise contrast than the other thresholds. This curve is shifted to the left of the threshold curve for the uncorrelated mask condition (U) by about 3 dB. This indicates that although the noise contrast in each eye was the same in the two conditions, the effectiveness of the noise in elevating threshold was greater for the correlated condition. The curves for monocular noise (LE, RE) remain consistently above and parallel to the curve for binocular thresholds in uncorrelated noise.

*A test of single-channel models.* Both the Legge, and Campbell and Green models assume that monocular signals are algebraically summed prior to detection and that noise, uncorrelated between the eyes, is associated with the peripheral signals. Threshold is considered to be a signal-to-noise discrimination. The  $\sqrt{2}$  binocular improvement arises in Campbell and Green's model only if during monocular viewing detection is affected by noise from the stimulated eye alone. One way to accomplish this is to assume that the peripheral signals are random variables whose means *and* variances depend on stimulus contrast. In Legge's model, the square-root law arises from the peripheral squaring nonlinear element. Each model offers the same two predictions for the form of the binocular summation contour in the presence of correlated or uncorrelated noise masks. *First*, since the models include only one central mechanism that adds both signal and noise, and since it is known from the results presented in Fig. 3

that threshold contrast is proportional to noise contrast, *thresholds for all stimuli in the contour should be equally elevated by the noise*. The binocular summation contours measured in the correlated and uncorrelated conditions should have the same shape, as indexed by the summation parameter  $\sigma$  (equation 1). *Second*, because both models produce square-root law binocular signal summation, the effective noise contrast in the correlated condition is  $\sqrt{2}$  times higher than effective noise power in the uncorrelated condition. Since noise contrast and threshold contrast are proportional, the same ratio should hold between threshold contrasts in the two types of noise mask. That is, for all stimuli, *thresholds should be  $\sqrt{2}$  times higher in correlated than in uncorrelated noise*.

A multiple-channel model, on the other hand, would predict a different result. Stimuli in which both eyes view equal contrasts would be detected by channels with equal sensitivities to the two eyes. If these channels are assumed to sum signal and noise linearly, the model would make the same prediction as the Campbell and Green model with regard to threshold contrasts for binocular stimuli: a  $\sqrt{2}$  sensitivity ratio between correlated and uncorrelated noise conditions. Channels characterized by extreme ratios of monocular sensitivities, which would mediate detection of gratings of extreme interocular contrast ratios, should be masked to roughly the same extent by the two types of noise, because they would be insensitive to variations in the noise delivered to the dominant eye. Thus a multiple-channel model would predict that the threshold contours would not be the same shape in the two types of noise, since thresholds for binocular stimuli would be more elevated than thresholds for nearly monocular stimuli.

We measured binocular summation contours in the presence of correlated and uncorrelated noise. The r.m.s. contrast of the noise mask for each eye was 0.05, a level that dominates internal noise under our conditions (Fig. 3). Threshold contrasts for gratings masked by this noise were roughly four times higher than thresholds for the unmasked gratings. Trials with the two different types of noise were randomly intermixed during a session.

Initially, we obtained thresholds by the method of adjustment. Figure 4 shows results for observers J.K. (Fig. 4A) and M.G. (Fig. 4B). Thresholds for the correlated conditions are indicated by the squares and thresholds for the uncorrelated conditions by the circles. The data

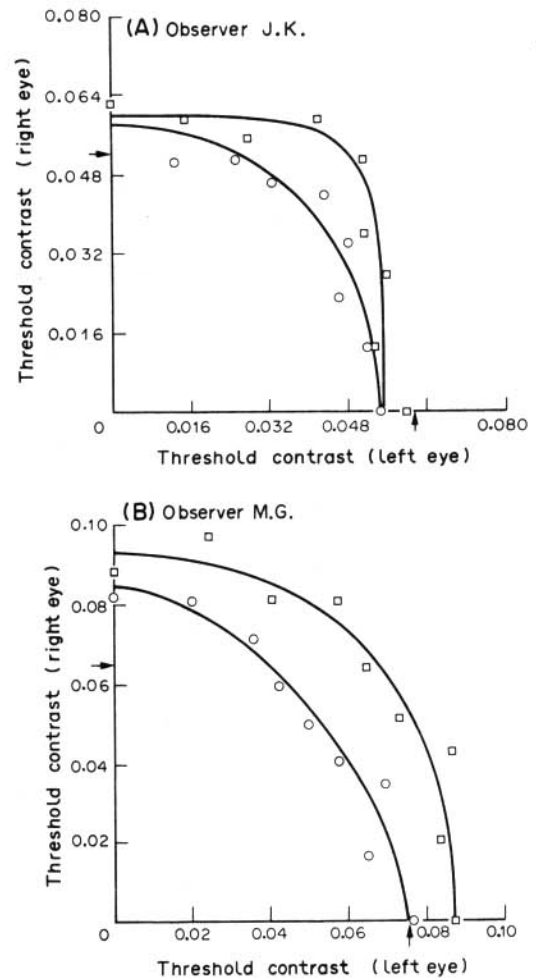


Fig. 4. The binocular summation contour measured in the presence of uncorrelated noise ( $\square$ ) and correlated noise ( $\circ$ ) for observers J.K. (A) and M.G. (B). Each data point is the mean of 8 adjustment settings. Arrows indicate the thresholds for monocular stimuli masked by monocular noise.

for both types of noise mask were fit to equation 1. The arrows on the axes indicate the threshold contrasts for monocular gratings masked by monocular noise. The resulting contours are clearly not of the same shape. For observer J.K.,  $\sigma$  for the contours measured in the correlated and uncorrelated noise were 5.3 and 2.1, respectively. The corresponding  $\sigma$  values for M.G. were 2.3 and 1.6. For binocular stimuli consisting of roughly equal left and right eye contrasts, the prediction of a  $\sqrt{2}$  sensitivity ratio between the two noise mask conditions was correct within experimental error. As expected from a multiple-channel model, as the interocular contrast ratio was made more extreme, the detectabilities of the two stimuli became roughly equal in the two types of noise (in a later section we will consider why they might not be precisely



equal). Note that the pattern of results for the two observers was similar, despite the difference in their characteristic values of  $\sigma$ . The two cases are representative of the nine such measurements made on five subjects. The mean value of  $\sigma$  in correlated noise was 3.8 (range: 2.3–5.3), and the mean in uncorrelated noise was 1.7 (range: 1.3–2.1). In all individual cases, the value in correlated noise was higher than the value in uncorrelated noise.

The results of the measurements made using the method of adjustment were suggestive, so to put the argument on firmer statistical footing we repeated this experiment using a 2IFC staircase procedure. We measured thresholds in each of the two noise conditions for three stimuli—the two monocular stimuli and the binocular stimulus in which both eyes view equal contrast. Staircases for the 6 conditions were interleaved in a single session. Three observers, M.P., M.G. and P.A., participated in 6 staircase sessions, each conducted on a different day. We separately analyzed each daily threshold estimate. The value of interest is the degree to which the masking effectiveness of correlated noise exceeds that of uncorrelated noise, which we take as the ratio of the thresholds in the two masking conditions.

For each observer, across the 6 sessions, we obtained 18 sensitivity ratios, 12 for monocular stimuli and 6 for binocular stimuli. The data for the monocular stimuli presented to the left and right eyes were not different and were therefore combined. Figure 5 shows the pooled data for all three observers in histogram form. The upper histogram shows the distribution of ratios between the thresholds in correlated and uncorrelated conditions for binocularly-viewed gratings; the lower histogram presents the ratios for the monocular stimuli. We placed the value for the correlated condition in the numerator of each ratio, so ratios greater than 1 (positive dB values) represent cases in which the threshold was higher in correlated noise. The mean for the 18 binocular ratios in the upper histogram was 3.04 dB (median 3.4), while the mean for the 36 monocular ratios in the lower histogram was 1.08 dB (median 1.45). The binocular ratios significantly exceed the monocular ratios both for the pooled distributions and for the individual distributions for each observer (Mann-Whitney  $U$ -test,  $P < 0.05$ ). Correlated noise thus had a more marked effect on the detection of binocular than of monocular stimuli. For binocular stimuli, the ratio was almost exactly

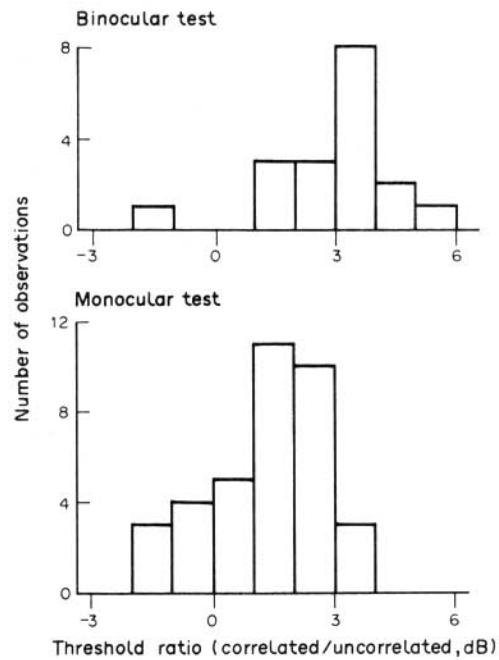


Fig. 5. Histogram showing pooled data for three observers. The sensitivity ratio is the ratio between thresholds in the correlated and uncorrelated masking conditions, in dB. The upper histogram indicates the sensitivity ratios for binocular gratings, and the lower histogram gives the sensitivity ratios for monocular gratings. On average, correlated noise elevated monocular thresholds 1.08 dB more than uncorrelated noise did; correlated noise elevated binocular thresholds 3.04 dB more than uncorrelated noise.

the  $\sqrt{2}$  (3 dB) predicted. For monocular stimuli, the effect was smaller.

Thus the results of our masking studies show that the shape of the binocular summation contour depends on the type of masking noise employed, a result at variance with the predictions of either single channel model. For binocular test targets, the threshold ratio was close to the  $\sqrt{2}$  predicted by these models, but for monocular test targets the effect was very small. This suggests that binocular targets were detected by mechanisms like those postulated by the single-channel models, but that monocular targets were detected by *additional* mechanisms preferentially sensitive to monocular stimuli.

#### *Effects of adaptation on binocular summation*

Monocular adaptation to a grating elevates the threshold for detection of a similar grating in either eye, although the magnitude of the aftereffect is less in the unadapted eye (Blakemore & Campbell, 1969). This partial interocular transfer cannot easily be accounted for by models like that of Legge, and Campbell and

Green, which postulate a single binocular channel, since such models would presumably predict complete interocular transfer, at least if adaptation is confined to points at or after the site of binocular combination. The incompleteness of interocular transfer has been taken to imply that both monocular and binocular neurons are involved in the aftereffect (e.g. Blake et al., 1981a). However, if *purely* monocular neurons provide a detection channel, interocular transfer would not be expected, since adaptation of one eye should not affect monocular channels sensitive only to the other eye. Blake et al. (1981a) deal with this problem by postulating that perceptual judgements are based on the pooled responses of monocular and binocular neurons. According to this kind of *averaging model*, the reduced magnitude of the threshold elevation in the unadapted eye is due to influence of unadapted, purely monocular neurons during testing. This is thus a single-channel model (since a single pooled response is used for detection) that involves multiple binocular mechanisms varying in ocular dominance.

In this experiment, we examined the effects of monocular adaptation to a high contrast grating on the detectability of stimuli of different interocular contrast ratios. If it is assumed that the extent to which a channel can be adapted by a stimulus is monotonically related to its sensitivity to that stimulus, an assumption supported by psychophysical data (e.g. Blakemore & Campbell, 1969), then a multiple-channel model predicts that monocular adaptation should result in threshold elevation being greatest for monocular stimuli presented to the adapted eye, least for monocular stimuli presented to the unadapted eye, and intermediate for binocular stimuli. Since nearly monocular channels would be most affected by adaptation, one would also expect binocular summation to be greater after adaptation. The averaging model of Blake and his colleagues makes similar predictions for the degree of threshold elevation for different test targets; it is unclear whether this model would predict an alteration in binocular summation after adaptation.

We collected adaptation data for a range of low and moderate spatial frequencies. Data for observers J.A.M. and J.K. are shown in Fig. 6A and B. Each observer viewed gratings of 6 c/deg. The horizontal and vertical axes give the contrast of the left and right eye's components of the gratings. We measured binocular summation contours both before and after

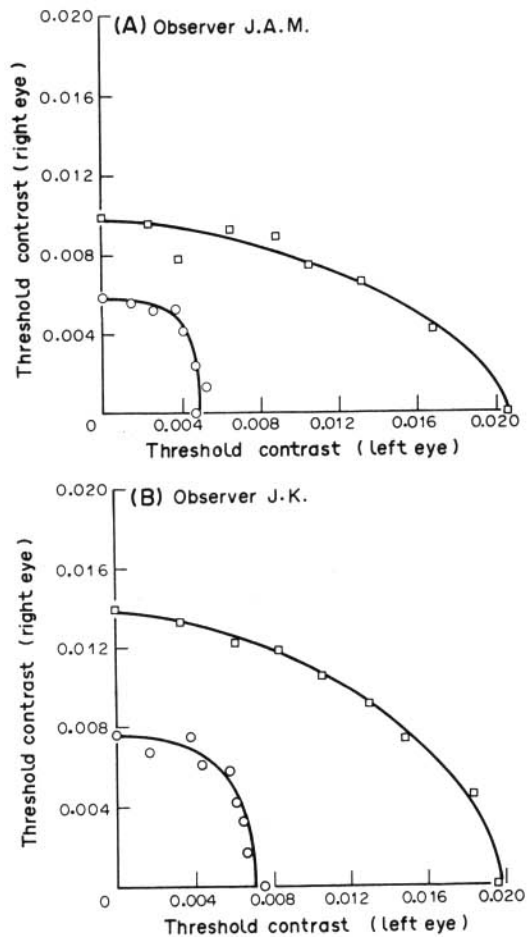


Fig. 6. Contrast thresholds for observers J.A.M. (A) and J.K. (B) before (○) and after (□) adaptation of the left eye to a 6 c/deg grating of 40% contrast. The two axes indicate the contrasts of the left and right eye's components of the gratings. Each data point represents the mean of 8 adjustment settings. All four data sets are fit to equation 1 as described in the text.

adaptation of the left eye. Preadaptation threshold contrasts are shown by the circles; the squares indicate the threshold contrasts measured following adaptation. Elevation of contrast threshold was greater for monocular stimuli presented to the adapted eye than for monocular stimuli presented to the unadapted eye, and the threshold contour is therefore asymmetric following adaptation. The change in shape cannot, however, be simply described as a scaling of the basic contour, such as would be produced by reducing the gain signals from one eye. In this case the summation parameter  $\sigma$ , determined by the *normalized* thresholds, would be unchanged by adaptation. All four sets of data were fit to equation 1. Before adaptation, the parameter  $\sigma$  was 3.1 for J.A.M. and 2.7 for J.K.; after adaptation, the  $\sigma$  values were 1.6 and

1.7. Monocular adaptation thus substantially increases the amount of binocular summation.

These data can be visualized another way, as shown in Fig. 7. Threshold elevation (in dB) is plotted against the interocular contrast ratio of the test stimulus (also in dB). The circles indicate threshold elevation following adaptation of the left eye. The threshold for the adapted eye was elevated substantially more than that for the unadapted eye, and thresholds for binocular stimuli were elevated to an intermediate degree, as predicted by the multiple-mechanism models. The threshold elevations in the adapted eye were 12.9 dB for J.A.M. and 8.3 dB for J.K. The elevations in the unadapted eye were 4.5 dB for J.A.M. and 5.1 dB for J.K. We observed both interocular differences in threshold elevation and the changes in binocular summation of roughly the same magnitude under all the adaptation conditions we studied for these and four other observers.

Thus the data on interocular transfer of adaptation seem to support models involving multiple binocular mechanisms. It might be possible to revive a single-channel model by supposing that adaptation could have effects both at and prior to the binocular summing point. If adaptation altered the gain of the monocular channel, partial interocular transfer would result. However, under these conditions, binocular summation would not be altered by adaptation, and the value of the summation parameter  $\sigma$  would be unchanged. Moreover, there is physiological evidence that adaptation-induced threshold elevation is minimal at monocular levels of the visual system (Movshon & Lennie, 1979; Ohzawa, Sclar & Freeman, 1985).

#### The distribution model

A model of binocular interaction must account for several observations about binocular summation, masking, and interocular transfer. It must account for binocular summation contours well fit by a power summation equation (Figs 1 and 2). Data from several different sources, such as the partial interocular transfer of the threshold elevation aftereffect, suggest that a simple single-channel model may be incorrect. If the envelope of several channels determines the form of binocular summation



Fig. 7. The adaptation data presented in Fig. 6, replotted to show threshold elevation in dB for stimuli of different interocular contrast ratios. Negative dB values of interocular contrast ratio indicate cases in which the left eye viewed a higher contrast than the right eye and positive values indicate cases in which the right eye was presented with the larger contrast.

contours, then a model must specify the relationship among channels in terms of their relative sensitivities to the two monocular signals. The specified relationship must account for the observation that binocular sensitivity is typically  $\sqrt{2}$  higher than monocular sensitivity. Finally, since there is evidence to suggest that visual cortical neurons which vary in their relative responsiveness to the two eyes may provide the substrate for binocular summation, it would be advantageous for the model to be consistent with physiological data. We have developed such a multiple-channel model, the *distribution model*.\*

*Differential sensitivity and ocular dominance.* It seems reasonable to suppose that the sensitivity of a neuron is related to the number and effectiveness of the inputs it receives. Suppose that each neuron can accept a fixed, limited number of inputs. Neurons would then obtain their ocular dominance signatures, or differential sensitivities to the two monocular

\*Our use of this term should be distinguished from the *distribution-shift* model of visual aftereffects proposed by Osgood and Heyer (1952) and subsequently elaborated by others, such as Mather and Moulden (1980).

signals, by allocating these inputs in different proportion to the right and left eyes. The function relating performance to an allocated resource of this sort is known as a performance-resource function (Norman & Bobrow, 1975). For a binocular summation channel, this function relates the channel's sensitivity, or responsiveness, to a monocular signal ("performance") to the proportion of inputs arising from that eye ("resource"). It thus specifies the relationship among the relative sensitivities to the two monocular signals of different channels.

There are no data to indicate what the performance-resource function of a channel should be; however, if we assume that each input has an independent Poisson distribution, the sensitivity of a channel would increase as the square root of the resource allocated.\* A more general form of this assumption suggests that a plausible candidate for the performance-resource function is a power function, with an exponent near 0.5. The distribution model thus takes the relative sensitivity,  $S$ , of a channel to a monocular signal as:

$$S = p^\delta; \quad 0 < \delta < 1; \quad (2)$$

where  $p$  is the proportion of inputs arising from a particular eye and  $\delta$  is a parameter which determines the efficiency of the utilization of that resource. When inputs to a channel are independent Poisson-distributed random variables,  $\delta = 0.5$ . As  $\delta$  decreases, the efficiency of  $p$  increases. When  $\delta = 0$ , maximum sensitivity is conferred on a channel by one input. This could occur if the noise associated with each input were perfectly correlated with that associated with all other inputs. When  $\delta = 1$ , channel sensitivity is simply proportional to the number of inputs, as if all noise limiting sensitivity were intrinsic to the channel and variability in the input signals were irrelevant.

*Shape of the binocular summation contour.* If we assume that binocular summation within each ocular dominance channel is linear (e.g. Ohzawa & Freeman, 1986a), knowledge of the performance-resource function allows us to predict the shape of the binocular summation contour. Each channel is characterized by a pair

of values,  $(p, 1 - p)$ , representing the proportion of inputs to the channel from the right and left eyes. Given  $\sigma$ , the sensitivity of each channel to the monocular signals can be determined by equation 2, and the reciprocals of these sensitivities are the normalized monocular threshold contrasts for each channel. Figure 8 illustrates the threshold functions for a family of linear channels for  $\delta = 0.5$ . Each line has a slope equal to  $-p^\delta/(1 - p)^\delta$ , and a y-intercept equal to  $1/p^\delta$  (see Appendix II). Since the distribution model excludes strictly monocular channels (see below), the distribution of  $p$  approaches but does not include values of 0 and 1.

We suppose that a particular interocular contrast ratio optimally activates one channel, characterized by a value of  $p$  (the proportion of inputs received from one eye). Each interocular contrast ratio produces a pattern of excitation across the family of channels; the peak of this excitation pattern determines threshold. Consider Fig. 8. If a line corresponding to a given interocular contrast ratio is drawn from the origin, the channel optimally activated by this stimulus is the one intersected first by the line; this channel's threshold function is perpendicular to the radius describing the stimulus. The observer responds when the output of the channel most sensitive to the stimulus exceeds a criterion value.

The envelope of the functions describing the ocular dominance channels traces a contour resembling the one generated by equation 1. According to this equation, the shape of a contour is characterized by the summation

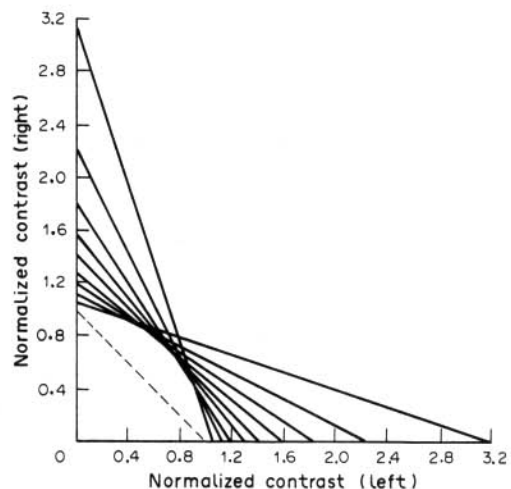


Fig. 8. The elements of the distribution model. A family of linear functions representing the sensitivity of different ocular dominance channels in the distribution model. See text for details.

\*Consider the sensitivity of a channel to be determined by its signal-to-noise ratio. The mean and the variance of a Poisson distributed random variable are equal. The mean of the sum of  $N$  inputs to a channel is proportional to  $N$ , while the standard deviation would be proportional to  $\sqrt{N}$ ; the signal to noise ratio would thus equal  $\sqrt{N}$ .



parameter,  $\sigma$ . We show in Appendix II that for each value of  $\delta$ , there is a value of  $\sigma$  such that the linear functions generated by the parameter  $\delta$  and equation 2 are tangent to the curve generated by  $\sigma$  and equation 1.

$$\delta = (\sigma - 1)/\sigma. \quad (3)$$

When  $\delta$  is 0.5,  $\sigma$  is near 2. ( $\sigma$  would be exactly 2 if the distribution of  $p$  included the values 0 and 1). Values of  $\sigma$  near 2 are typical of many binocular summation contours, and when  $\sigma = 2$ , the sensitivity to a binocularly-viewed grating is  $\sqrt{2}$  times the sensitivity to a monocularly-viewed grating. The assumptions of the distribution model thus account for this commonly reported binocular improvement in sensitivity in a way very different from the Legge or Campbell and Green models. One virtue of the distribution model is that it can also easily account for binocular-to-monocular sensitivity ratios that differ from  $\sqrt{2}$ ; this is accomplished by varying the parameter  $\delta$  or limiting the distribution of  $p$ .

*Distribution of ocular dominance channels.* We simulated the effects of monocular adaptation on the shape of the binocular summation contour to test whether the distribution model could plausibly account for the form of the data (Anderson, 1982). Using reasonable assumptions about adaptation, the model generates values very similar to those obtained from real observers. By assuming a power function relationship between the sensitivity of a channel and the extent to which it can be adapted, substantial interocular transfer results even when there are channels that are nearly monocular ( $p$  varying from 0.05–0.95). Our noise masking data also suggest that the distribution of ocular dominance channels does not include purely monocular channels. Recall that varying the interocular correlation of masking noise causes a reliable, if modest change in the detectability of monocular stimuli (Fig. 5). This suggests that such stimuli are detected by channels that have small but measurable sensitivity to inputs from the other eye.

The distribution of ocular dominance of striate cortical neurons in both monkeys and cats includes neurons that are strictly monocularly excitable (Hubel & Wiesel, 1962, 1968; Macy, Ohzawa & Freeman, 1982). It is possible that monocular channels exist but can be adapted and masked (perhaps through inhibitory processes) by stimuli presented to the ineffective eye. Bishop (1973) and Ohzawa and Freeman

(1986a, b) discuss the evidence for inhibitory interocular influences of this sort, but it is not known whether interocular adaptation can be demonstrated physiologically in monocular neurons (cf. Cogan, 1987). Alternatively, signals from monocular neurons may be inaccessible at the stage of visual processing corresponding to the detection channel. Monocular neurons in the monkey striate cortex are mostly confined to layer IV, and probably do not have axons of extrinsic distribution (Hubel & Wiesel, 1968; Lund & Boothe, 1975); monocular neurons in primate extrastriate visual cortex are very rare (e.g. Zeki, 1978).

The distribution model does not specify a particular number of channels; it merely requires that there be a sufficient number to yield binocular summation contours of the smoothness shown. There is no evidence for small numbers of specific classes of striate cortical neurons differing in ocular dominance (Macy et al., 1982). The ocular dominance parameter,  $p$ , in the distribution model is flexible;  $p$  can be varied in the extent to which it approaches 0 and 1. The distribution of the values of  $p$  need not be continuous; it can also be discrete. In this way, the distribution model could incorporate experimental evidence that might be obtained for a specific limited number of channels.

*Probability summation.* Any model involving multiple detection channels must consider the possibility that the channels are independently perturbed by noise and that probability summation contributes to detection thresholds. The model most often used to calculate probability summation is the two-state model. The version employed by Graham, Robson and Nachmias (1978) and by Watson et al. (1980) assumes that the psychometric function for a detection channel is described by the equation suggested by Quick (1974). We used this model together with the assumptions of the distribution model to simulate the effects of probability summation on the shape of the binocular summation contour. These effects depend on the slope of the underlying psychometric function (which we fixed at the generally accepted value of 4), the number of channels and the underlying value of  $\delta$ . With  $\delta = 0.5$ , our simulations indicate that probability summation among the 9 channels illustrated in Fig. 8 would markedly alter the shape of the contour ( $\sigma$  changes from 1.8 to 1.2, closely approaching apparent linear summation). Probability summation among as few as 3 channels still yields  $\sigma$  values less than those measured for

observers. Even if  $\delta$  is very small, probability summation among a few channels yields  $\sigma$  values much less than those describing data for real observers. Our model must therefore postulate that the effects of probability summation in determining the binocular summation contour are minimal.

It is presently fashionable to account for psychophysical data on the detectability of compound gratings by postulating multiple spatial frequency channels (see Graham, 1980). The variability of each channel's responses is uncorrelated with that of other channels, and probability summation can thus influence the detectability of a stimulus. In order for probability summation to occur, the variability across channels must be to some degree uncorrelated, for if it were perfectly correlated, no advantage would result from consulting signals in more than one channel. It is unlikely, however, that ocular dominance channels would be characterized by uncorrelated variability. The elements composing the channels share a common preference for the location and spatio-temporal character of the stimulus, and thus must share many common inputs. This would ensure that noise across ocular dominance channels be at least partly correlated. We also have experimental evidence against stochastic independence among ocular dominance channels. Recall that we measured the binocular summation threshold contour in the presence of visual noise that was uncorrelated between the eyes. Such noise must automatically *increase* the correlation among channels with similar ocular dominance values, and thus reduce any effects of probability summation, lowering the summation parameter  $\sigma$ . However, for each observer, the value of  $\sigma$  obtained under these conditions was very similar to the value obtained under unmasked conditions. We concluded that activity in channels with similar ocular dominance values is correlated, even when only intrinsic sources of variability are present, and that probability summation makes little or no contribution to the summation contours observed. The distribution model thus excludes any influence of probability summation.

## DISCUSSION

### *Models of binocular summation*

Models of binocular summation have many forms and flavors, and we will consider five that instantiate the interesting varieties in the

literature. The models differ both in the number of mechanisms they contain, and in the number of channels to which those mechanisms send signals; recall that we distinguish mechanisms (neural elements in the visual pathway) from channels (the combination of a group of mechanisms with a device for making detection decisions; see footnote on p. 1116 and Graham, 1980). The models are:

- Campbell and Green's (1965) linear summation model, a single-mechanism, single-channel model;
- Legge's (1984b) quadratic summation model, also a single-mechanism, single-channel model;
- Cogan's (1987) model, a two-mechanism, single-channel model (this model is similar in character to another proposed by Cohn, Leong & Lasley, 1981);
- Blake et al.'s (1981a) averaging model, a multiple-mechanism, single-channel model;
- Our own distribution model, presented above, a multiple-mechanism, multiple-channel model.

Other kinds of model have been proposed to explain one or another aspect of binocular function, but we are unaware of any that can account for much of the basic data on binocular summation (Blake & Fox, 1973; Blake et al., 1981b).

### *The binocular summation contour*

All five models either explicitly or implicitly account for the observation that the binocular summation contour can be described by a power summation rule with an exponent near 2. Both Campbell and Green's model and Legge's model were designed explicitly to deal with data related to this basic fact of binocular summation, so it is no surprise that they predict it. It must be noted that Campbell and Green's model is imprecise on one key point: for the signal-to-noise calculation to yield the desired  $\sqrt{2}$  improvement in sensitivity, the binocular mechanism must be able to ignore noise arising in the unstimulated eye during monocular stimulation (otherwise the model predicts not a factor of  $\sqrt{2}$  but a factor of 2 improvement). The original description includes no mention of how the model is to achieve this behavior, which is by nature neither single-channel nor perfectly binocular.

The averaging model makes no explicit prediction about binocular summation, but is

presented in sufficiently general terms that it could certainly be made to predict this data.

Cogan's model and our own both explicitly fit binocular summation contour data. Cogan's conditions were rather different from those used in the rest of the studies (he measured the detectability of whole-field changes in the luminance of a textured target), and his contours, if fit with the power summation equation, would have exponents nearer 1 than 2, at least for conditions in which the targets were of the same sign in the two eyes. On the other hand, the distribution model explicitly relates the quadratic binocular summation contour to the square-root performance-resource function expected of a process limited by independent monocular sources of noise; exponents near 1 carry the interpretation that the noise limiting performance has a source central to the point of binocular combination.

#### *Masking by visual noise*

Both single-mechanism models fail to account for the way that different forms of binocular visual noise affect the shape of the binocular summation contour. Because both are noise-limited, and both have but a single binocular site at which signals are summed, each predicts that any of our masking conditions should have elevated threshold for all test targets to the same degree; this is not the case (Figs 4 and 5).

The averaging model is not formulated in such a way that explicit predictions about the effects of masking noise can be made, because the nature of the "averaging" is not explicit. Assuming that the postulated pooling is the result of linear summation of signals across mechanisms, the model makes the same prediction for the masking case as the single channel models. This is due to the fact that signals from all mechanisms are pooled before making detection decisions, and threshold is based on the average activity across mechanisms. Thus, since thresholds for gratings of all interocular contrast ratios are determined by the same signals, and the noise uniformly perturbs those signals, it would seem that this model would predict that the shape of the summation contour would be unchanged by masking. This, of course, depends on the pooling assumption; it might be possible to formulate a version of the model using different pooling rules, or incorporating a purely binocular process (Wolfe & Held, 1981), that was able to fit our data.

Cogan's model has two distinct points of early nonlinear interaction between signals from each eye, a multiplicative "fused" mechanism and an "either eye" mechanism modified by interocular shunting inhibition. Suitably-weighted combinations of these mechanisms might be able to predict the shape of the masking results. However, a consistent feature of our results was that thresholds for binocular targets in correlated noise were  $\sqrt{2}$  higher than these thresholds in uncorrelated noise (Figs 3 and 4). This result is readily predicted by models in which signal combination between the eyes is additive, but would not emerge easily from a highly nonlinear model like Cogan's.

The distribution model accounts for the noise masking data. According to this model, stimuli in which both eyes view equal contrasts are detected by channels that possess equal sensitivities to the two eyes. These channels linearly sum the signal and noise. The model makes the same prediction as the single-mechanism models with regard to threshold contrasts for masked binocular stimuli, that is, a  $\sqrt{2}$  sensitivity ratio between correlated and uncorrelated noise conditions. Channels characterized by extreme ratios of monocular sensitivities, which are assumed to mediate detection of gratings of extreme interocular contrast ratio, should be more equally masked by the two types of noise fields, since they are relatively insensitive to the noise in the nondominant eye. Threshold contrasts are predicted to be similar in the two masking conditions. These predictions are confirmed by the data (Figs 4 and 5).

#### *Interocular transfer of adaptation*

Under the assumption that adaptation occurs only in the binocular portions of the processing chain, neither the Campbell and Green model nor the Legge model predict partial interocular transfer. If early monocular portions of the pathway could also be adapted, partial interocular transfer would result. But, because they have only a single site of binocular combination, it is difficult to see how these models could account for the fact that binocular summation *improves* after monocular adaptation (Fig. 6).

Both Cogan's model and the averaging model were devised to account for the phenomenon of partial interocular transfer, and our interocular transfer results are consistent with their predictions. Cogan's model achieves partial transfer by the persistence of the interocular shunting

inhibitory interaction, while the averaging model uses more conventional "fatigue" models of adaptation. Although neither model specifically predicts the improvement in binocular summation after monocular adaptation, such a result could emerge from pooling structures like those built into the models. The particular strength of the averaging model is that it accounts for partial interocular transfer despite the physiologically-plausible inclusion of purely monocular mechanisms; Cogan's model allows no unmodified monocular signal to enter the detection channel.

Partial interocular transfer of threshold elevation is accounted for in the distribution model by assuming that the distribution of ocular dominance channels does not include pure monocular channels. Channels can, however, receive as few as 5–10% of their inputs from an eye and still show substantial threshold elevation following adaptation of either eye, as our simulations demonstrate. Thus the distribution model can postulate channels which are nearly monocular and still account for partial interocular transfer; purely monocular channels, however, cannot exist in this model.

#### *Nature of the ocular dominance channel*

It appears that among the models that make explicit predictions, only the multiple-mechanism, multiple-channel distribution model presently offers a satisfactory account of all of our results. It might be that a fully fleshed-out version of the averaging model is workable, but it seems clear that models positing only one site of binocular combination fail to deal with several results.

The distribution model requires the existence of multiple independent *ocular dominance channels*, whose general structure resembles that of other channels commonly used to model visual detection (Graham, 1980). Ocular dominance channels, however, must differ in important ways from other psychophysically determined channels. According to current theories, at an early stage in visual processing, the spatial frequencies present in a stimulus are detected by multiple channels; each channel is assumed to respond to a relatively narrow range of spatial frequencies (see Graham, 1980, for review). At threshold contrasts, gratings that differ sufficiently in their spatial frequencies can be discriminated (e.g. Nachmias & Weber, 1975). In fact, it has been suggested by Watson and

Robson (1981) that if two spatial frequencies can be perfectly distinguished at threshold, they must be detected by different channels. These investigators suggest that spatial frequency channels are *labelled lines*, which signal not only the presence of a stimulus but also its identity.

Ocular dominance channels, on the other hand, are certainly not labelled lines. The difficulty experienced in discriminating the eye-of-origin of monocular stimulation is well documented, and it is almost impossible to discriminate which eye receives the higher of a dichoptic pair of contrasts. Thus ocular dominance channels cannot provide much information concerning the dimension along which they are distributed. This of course makes sense, for the simple reason that we can imagine no important visual function for which it would be necessary to know the eye of origin of a monocular target, or the eye receiving higher contrast stimulation. In this respect, then, ocular dominance channels must be unlike spatial frequency channels as these are usually conceived. In addition, we have already discussed our belief that ocular dominance channels, unlike spatial frequency channels, are not perturbed by independent variability and that the ocular dominance channel system therefore does not display the influence of probability summation.

Ocular dominance channels would thus differ importantly from other kinds of psychophysical channel, but we believe that the evidence for their existence is nonetheless compelling. We must therefore suppose that the conventional conception of a channel does not apply in its entirety to this case. The reader disturbed by this particular flavor of "pseudo-channel" might wish to take refuge here in some form of the averaging model. Certainly the pooling aspects of the averaging model are useful in explaining why observers fail to make utrocular discriminations, and how they can have monocular visual mechanisms and yet show interocular transfer. The mechanisms averaged by the averaging model could have many of the characteristics of those in the distribution model, and this could confer much of the same flexibility on the averaging model. But however the issue is dealt with, it is clear that the facts of binocular summation, masking and adaptation cannot be accounted for by a single binocular mechanism, and that some more elaborate model is required.



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**APPENDIX I**

*Goodness of fit*

In this appendix we describe the statistic we used to evaluate the fit between the observed binocular summation and equation 1. Threshold contrasts were converted from Cartesian coordinates to polar coordinates so that minimization (in linear units) between the threshold contrasts and the thresholds predicted by equation 1 was done along lines passing through the origin. We minimized the following statistic using the STEPIT subroutine (Chandler, 1965) to adjust the value of the parameters for equation 1:

$$X^2 = \sum_{i=1}^m \left[ \frac{(\bar{x}_i - \mu_i)}{(s_i/\sqrt{n-1})} \right]^2;$$

where  $m$  is the number of stimulus conditions,  $\bar{x}_i$  is the mean of  $n$  observations made for a stimulus,  $\mu_i$  is the value fit (for example, to equation 1), and  $s_i$  is the standard deviation of the  $n$  observations. Under the assumption that each observation is a sample in a normal distribution, this statistic is the sum of  $m$  independent  $t^2$  random variables, and is distributed approximately as  $\chi^2$  with  $m - df$  degrees of

freedom, where  $m$  is the number of stimuli and  $df$  is the number of estimated parameters, 3 in the case of equation 1. A test of goodness of fit based on  $X^2$  is actually conservative relative to  $\chi^2$ . For a criterion probability of 0.05, values of  $X^2$  less than 12.59 indicate satisfactory agreement between the observed and predicted values.

**APPENDIX II**

*Relation Between Power Summation and the Distribution Model*

The distribution model proposes a relationship between the  $\sigma$  curve:

$$x^\sigma + y^\sigma = 1; \tag{II-1}$$

and a family of lines, defined by the pair  $(p, 1 - p)$ , where  $p$  is the proportion of inputs a mechanism receives from the right eye and  $(1 - p)$  is the proportion arising from the left eye;  $p$  varies between 0 and 1. Each linear mechanism is characterized by a pair of monocular sensitivities,  $p^\delta$  and  $(1 - p)^\delta$ , with  $\delta$  being a parameter that determines the efficiency of  $p$ .

This appendix presents the derivation of the equation.

$$\delta = (\sigma - 1)/\sigma; \tag{II-2}$$

which expresses the relationship of interest. Fix  $\sigma$  and obtain the equation for a tangent line to equation 1, passing through the point  $(x_0, y_0)$  on the  $\sigma$  curve. First, calculate the slope at  $(x_0, y_0)$ :

$$\sigma x^{\sigma-1} + \sigma y^{\sigma-1} y' = 0; \tag{II-3}$$

$$y' = -x_0^{\sigma-1}/y_0^{\sigma-1}, \tag{II-4}$$

which is the slope. The equation of the tangent line is:

$$y - y_0 = \{-x_0^{\sigma-1}/y_0^{\sigma-1}\}(x - x_0); \tag{II-5}$$

$$y - y_0 = \{-x_0^{\sigma-1}/y_0^{\sigma-1}\}x + x_0^\sigma/y_0^{\sigma-1}. \tag{II-6}$$

By equation 1,  $x_0^\sigma = 1 - y_0^\sigma$ , therefore we can write:

$$y - y_0 = \{-x_0^{\sigma-1}/y_0^{\sigma-1}\}x + 1 - y_0^\sigma/y_0^{\sigma-1}; \tag{II-7}$$

$$y = \{-x_0^{\sigma-1}/y_0^{\sigma-1}\}x + 1/y_0^{\sigma-1}. \tag{II-8}$$

The equation can be written as:

$$y_0^{\sigma-1}y = -x_0^{\sigma-1}x + 1. \tag{II-9}$$

Define  $p_0 = y_0^\sigma$ , so  $p_0^{1/\sigma} = y_0$ , and:

$$p_0^{(\sigma-1)/\sigma} = y_0^{\sigma-1}. \tag{II-10}$$

Since  $x^\sigma + y^\sigma = 1$  by the model, and since  $p_0 = y_0^\sigma$ ,  $1 - p_0 = x_0^\sigma$ , so  $(1 - p_0)^{1/\sigma} = x_0$ , and:

$$(1 - p_0)^{(\sigma-1)/\sigma} = x_0^{\sigma-1}. \tag{II-11}$$

The equation for the tangent line equation 9) becomes:

$$p_0^{(\sigma-1)/\sigma}y = -(1 - p_0)^{(\sigma-1)/\sigma}x + 1. \tag{II-12}$$

Letting  $\delta = (\sigma - 1)/\sigma$  (equation 2), we have the desired expression:

$$yp^\delta + x(1 - p)^\delta = 1. \tag{II-13}$$

This relationship between  $\delta$  and  $\sigma$  means that the family of lines generated by the parameter  $\delta$ , which describe the channels postulated by the distribution model, are all tangent to the equation used to fit the binocular summation contour. The distribution model asserts that each interocular contrast ratio is detected by that channel whose  $\delta$ -function is perpendicular to the radius describing the stimulus, since it is this channel that is most sensitive to the stimulus.