Differences between stereopsis with isoluminant and isochromatic stimuli

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Contrast thresholds for stereoscopic depth identification (crossed or uncrossed) were measured as a function of disparity by use of isoluminant (red-green) and isochromatic (yellow-black) 0.5 cycles/deg Gabor patches. For the purposes of comparison, stimulus contrasts were scaled by their respective detection thresholds. The Gabor patches could be either vertically or horizontally oriented. It was found that the disparity dependence of the depth-identification contrast thresholds was similar for both chromatic and luminance patterns if the stimuli were vertically oriented, with the overall level of performance worse for the chromatic patterns by a factor of ~ 2 (6 dB). With horizontal patterns this difference was much larger, by a factor of ~ 7 (17 dB). These results suggest first that stereopsis in the absence of luminance cues is supported by a less-contrast-sensitive linear mechanism than that which supports stereopsis in the presence of luminance cues and second that the corresponding nonlinear chromatic stereo mechanism is either nonexistent or very weak. The implications of these data for previous studies of stereopsis at isoluminance is discussed.

Key words: color, stereopsis, contrast sensitivity, isoluminance, binocular vision. © 1995 Optical Society of America

1. INTRODUCTION

Stereopsis is frequently cited as an example of a visual ability that is degraded at isoluminance.¹ Yet more than 20 years of empirical and theoretical studies have failed to resolve the precise nature of this degradation.^{1–16} The point of view summarized by Gregory⁶ and based on the original evidence of Lu and Fender² and Comerford⁵ is that stereopsis with random-dot patterns is effectively destroyed at (red-green) isoluminance, whereas it is maintained with so-called figural stimuli such as lines and bars. This point of view has probably remained in the popular imagination because a demonstration of the disappearance of stereopsis with isoluminant randomdot patterns is often compelling.⁶ More-recent studies have suggested that, while subjects are still able to make correct judgments about stereoscopic depths at isoluminance, the quality of the depth percept is impaired. This quality reduction may take the form of a reduced stereoacuity^{10,11,13,14} or contrast sensitivity^{15,16} or simply a less solid stereoscopic surface.⁹ Other authors have suggested that a link exists between the spatial-frequency content of random-dot stereograms and the extent to which the stereoscopic surfaces they define are affected at isoluminance.17,18

In summary, it seems clear that something strange is happening at isoluminance that alters our perception of stereoscopic depth. What could be the cause of this strangeness? One possibility is that at isoluminance the effective stimulus contrast is reduced as a result of the overlap in spectral sensitivities of the longand middle-wavelength-sensitive cones. Scharff and Geisler¹⁵ tested this proposition for stereopsis by employing an equivalent-contrast metric that used a model of the optical and physiological properties of the eye and retina to equate the contrasts of isoluminant and isochromatic stimuli at the level of the photoreceptors.^{12,19} Using this metric, they found that for some of their subjects contrast thresholds for stereopsis were approximately equal at all levels of luminance contrast, including isoluminance. This result must, however, be doubly qualified. First, as Scharff and Geisler report, equal-contrast thresholds were found only in two subjects out of a total of six tested.¹⁵ Other subjects' thresholds either increased at isoluminance or were so high for luminance-based stereopsis that the color contrasts required for comparison were unobtainable on their equipment. Second, Simmons and Kingdom¹⁶ have shown that, when the contrasts of isoluminant and isochromatic stimuli are measured in terms of multiples of detection threshold, there is a clear deficit in performance in a stereoscopic depth-identification task at isoluminance. They found that, for the same stereo performance level to be obtained with isoluminant stimuli as with isochromatic stimuli, the isoluminant pattern had to be set to a higher contrast. Hence, a reduced effective contrast at isoluminance appears not to be the only factor in the performance reduction at isoluminance. A similar conclusion has been reached by a number of other authors for the relationship between the detection and direction discrimination of chromatic motion stimuli.²⁰⁻²³

The chief aim of this study is to understand the nature of the stereo performance loss at isoluminance, and the working hypothesis is that chromatic stereopsis exhibits disparity tuning and/or contrast sensitivity different from that of luminance stereopsis. We have already shown that, over the range of disparities from 0-60 arcmin tested in our previous study¹⁶ (corresponding to phase disparities of up to a half cycle of the Gabor carrier), the disparity tuning of the chromatic stereo mechanism is similar to the luminance stereo mechanism, but there is an overall reduction in contrast sensitivity when contrast is measured in multiples of detection threshold. Yet, in the random-dot stereograms commonly used as stimuli to demonstrate performance loss at isoluminance, the disparities are often large compared with the spatial-frequency content of the pattern, and the patterns themselves have a broad spatial-frequency and orientation bandwidth. Hence in this study we have investigated a range of stimulus disparities and orientations broader than those employed previously, while keeping in mind the necessary stimulus restrictions for avoiding luminance artifacts that are due to chromatic aberration.¹⁵ Contrast thresholds for stereoscopic depth identification were measured with both isochromatic and isoluminant Gabor patterns that were either vertically or horizontally oriented. The range of disparities employed extended up to 1.3 cycles of the carrier frequency. These experiments revealed important differences between the stereoscopic depth perception of chromatic and luminance patterns that have, to our knowledge, previously been unreported.

2. METHODS

A. Stimuli

The stimuli used were isoluminant and isochromatic Gabor patches consisting of a sinusoidal modulation in color or luminance contrast multiplied by a Gaussian envelope,

$$f(x, y) = L_0\{1 + m \exp[-(x^2 + y^2)/2\sigma^2)]\sin(2\pi\nu x)\}, \quad (1)$$

where f is the variation in luminance or chromaticity, x is distance along the horizontal, y is distance along the vertical, L_0 is the mean luminance or chromaticity, m is the contrast, σ is the standard deviation of the Gaussian modulation, and ν is the spatial frequency of the sinusoid. Stimuli were always in sine phase to avoid any change in the mean luminance or chromaticity during stimulus presentation. The spatial frequency of the patterns was always 0.5 cycles/deg, and σ was 1 deg, resulting in a spatial bandwidth of approximately 1.1 octaves (full width at half-maximum). These stimulus parameters were designed to minimize luminance artifacts in the chromatic stimuli that were due to chromatic aberration.¹⁵ The stimuli were either vertically oriented [as in Eq. (1)] or horizontally oriented [Eq. (1) with $\sin(2\pi\nu y)$ instead of $\sin(2\pi\nu x)$]. The stimuli appeared in a high-contrast white fixation annulus that was present throughout the experiment. The annulus was 1.8 arcmin (1 pixel) thick and had a radius of 3 deg. A pair of high-contrast vertical nonius lines, each 36 arcmin long and 1.8 arcmin (1 pixel) wide, was present both before, between, and immediately after stimulus presentation. These nonius lines served as an additional disparity reference and ensured that subjects' eyes were correctly positioned. The ensemble of fixation stimuli was designed to provide a strong depth reference at zero disparity (Fig. 1).

B. Apparatus

The stimuli were presented with use of a BARCO Calibrator monitor, driven by a VSG2/2 graphics controller (Cambridge Research Systems) mounted on a DELL 486D/33 platform. Stimulus separation was obtained using a pair of liquid-crystal shutters (Displaytech Inc.) that were mounted in a set of optometric trial frames. The shutters were driven from the graphics controller in such a way that the shutters alternately opened and closed at the start of every frame, thereby presenting alternate frames to each eye. The frame rate of the monitor was 160 Hz, resulting in a refresh rate of 80 Hz in each eye. This frequency is well above that required for flicker fusion in foveal vision, and, accordingly, no stimulus flicker was observed.

It is well known that interocular cross talk can be a problem when liquid-crystal shutters are used to separate stereo half-images in a setup such at this one. This cross talk is caused largely by slow phosphor decay that results in, say, the left-eye stimulus still being faintly visible when the right-eye shutter is in the open state. In a previous study it was shown that this cross talk was unlikely to be a problem in the measurement of simple detection thresholds.¹⁶ For higher-contrast presentations the cross talk would certainly have been visible. Control experiments indicated that the contrast of the cross talk was approximately 20 dB (factor of 10) lower than that of the actual stimulus. However, given the evidence that low-contrast stereoscopic signals have little effect on perceived depth in the presence of higher-contrast signals²⁴ and recent evidence for a contrast-similarity constraint on stereo matching,²⁵ we assume here that the cross talk did not significantly affect performance.

After passage through the shutter glasses the mean luminance at each eye was approximately 2 cd/m^2 . At this low photopic luminance the rod photoroceceptors were almost certainly not saturated, but the subjective method for determining the isoluminant point (see below) should have kept their contribution to a minimum (see Ref. 16 for a detailed discussion of this issue). The luminance of the fixation stimuli at the eye was approximately 10 cd/m². The size of the luminous part of the display was 16 deg wide and 11.5 deg high. The viewing distance was 114 cm. Experiments were carried out in a dark light-tight room. The display was viewed with natural pupils.²⁶



Fig. 1. Schematic perspective diagram of the stimulus configuration. Illustrated are the fixation annulus and nonius lines (one presented to each eye) as they would appear when fused, although the break between the nonius lines is only for illustrative purposes (they were abutting in the actual experiment). The Gabor stimulus appeared in front of or behind these reference markers. The nonius lines were not present during stimulus presentation, although the circle was. For dimensions and further details, see text.

C. Calibrations

Luminance calibrations were carried out with a UDT 265 photometer. The red and green guns of the display were carefully linearized before any data were collected, and the calibrations were periodically checked. During the course of data collection no significant drifts in the display properties were observed. The spectral properties of the stimulus were assessed with use of data obtained from a calibration of another monitor of the same make (phosphor properties vary little from monitor to monitor) and the manufacturer-supplied spectral transmission data for the shutter glasses. The CIE coordinates of the red and green phosphors were (x = 0.623,y = 0.340) and (x = 0.278, y = 0.584), respectively, before passage through the shutter glasses and (x = 0.614,y = 0.347) and (x = 0.270, y = 0.594), respectively, after passage through the shutter glasses.

D. Subjects

Subjects were the two authors. Both were color normal. One (FK) was emmetropic and the other (DS) wore his prescribed optical correction. Both subjects were highly experienced in stereoscopic depth discriminations.

E. Stimulus Generation and Color Contrast

In the descriptions that follow, two classes of stimulus were used: luminance stimuli and chromatic stimuli. For the luminance stimuli, modulation of the red and green guns of the monitor were in spatial phase, whereas for the chromatic stimuli they were in spatial antiphase. For both stimulus classes the contrasts reported are the Michelson contrasts [i.e., $(L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}})$] of the Gabor's carrier grating before multiplication of the Gaussian envelope. This measure of contrast was directly proportional to one based directly on the Gabor stimulus itself, such as $(L_{\max} - L_{\max})/L_{\max}$. The luminances, L, were those measured with the photometer. The contrasts defined in this manner were constrained to be equal on each gun, whatever the overall ratio of mean red to overall mean luminances. This ratio [the R/(R+G) ratiol could be independently adjusted, and it controlled the relationship between the mean luminances on each of the guns. Adjustments of this value from low to high would thus vary the color of the background field of the display from greenish through yellow to reddish.

F. Procedures

1. Isoluminance Setting

The isoluminant point was determined with the method of minimum motion.^{27,28} A slowly drifting (0.6 deg/s) sinusoidal chromatic grating of the same spatial frequency and size as the experimental stimulus was presented on the display. The color contrast of the grating was set at a value of 15%, which was easily visible but well below the maximum obtainable on the display. Subjects adjusted the R/(R + G) ratio in the display such that the drift speed appeared to slow. When the point of minimum drift speed was observed, the subject pressed a button to indicate his choice. This process was repeated ten times, and means and standard errors were calculated. The setting was made with the shutter glasses in position to account for their wavelength-dependent attenuation characteristics. Separate settings were made for

vertical and horizontal patterns, but no significant difference was found. The R/(R + G) values obtained for each subject were 0.53 and 0.57 for FK and DS, respectively.

2. Depth Identification

In the main series of experiments, stimuli were constructed with six disparities, three crossed and three uncrossed. One of these stimuli was presented at random in one of two temporal intervals, each 200 ms long, separated by a 1-s gap. The other interval was blank. Stimulus onset and offset were abrupt. Two temporal intervals were used for matching the uncertainty requirements of the depth task to those of the detection task,²⁹ thus allowing a valid comparison of the contrast requirements for each task. Irrespective of the interval in which the stimulus was presented, the subject was asked to judge whether the stimulus appeared to be in front of or behind the disparity reference. The nonius lines were always present except during stimulus presentation. In the course of the experiment, stimuli were presented at a range of color or luminance contrasts. This range was selected to bracket the required contrast threshold. A given experimental run consisted of six presentations at each of the six disparities and five contrasts together with 36 zero-contrast "catch" trials to probe for subject biases. There were thus 216 trials in each experimental run. The duration of a run was approximately 10 min.

In a later experiment (data presented in Fig. 5 below) only two disparity values were employed, one crossed, the other uncrossed. The number of presentations at each disparity and contrast was increased to ten in each experimental run. Consequently the run was shorter, at 120 trials (including 20 catch trials). A further elaboration in this experiment was that the phase of the Gabor pattern was randomized between +90 and -90 deg (i.e., positive and negative sine phase). This procedure was intended to reduce the buildup of strong afterimages in these high-contrast patterns.

In the final control experiment (data presented in Figs. 6 and 7 below), two disparities were again employed, but a single run now lasted 144 trials. The stimulus elaborations introduced here included either an interocular phase difference, where stimuli in positive and negative sine phase were presented to opposite eyes, or an interocular orientation difference, where horizontally and vertically oriented stimuli were presented to opposite eyes. In both cases there was an equal probability of the positive phase or the horizontal stimulus going to either eye during the course of the experiment. This precaution reduced the likelihood of cyclotorsional eye movements affecting performance and also prevented subjects from doing the task by determining which eye had seen which stimulus (i.e., some form of utrocular discrimination). In all cases, data from a number of runs were collated for constructing psychometric functions relating the proportion of "front" responses to the stimulus contrast.

3. Contrast Detection

Detection experiments were performed in concurrent sessions with the depth-identification experiments. In the detection experiments there were also two presentation intervals, in one of which the stimulus was presented. The subject was asked to decide whether the stimulus had appeared in the first or the second interval. During the course of a single experimental run, binocular³⁰ and monocular presentations were randomly interleaved. The stimulus configuration, stimulus duration, and number of trials (216) were exactly the same as in the main series of depth-identification experiments. Experiments were performed at eccentricities of 0, 30, 40, 50, and 80 arcmin, corresponding to disparities of 0, 60, 80, 100, and 160 arcmin, respectively. Values of detection threshold at intermediate eccentricities were obtained by interpolation.

G. Data Analysis

A maximum-likelihood procedure, similar to that employed by Watson,³¹ was used to fit the depth-identification and simple-detection psychometric functions with Weibull-Quick functions. A "bootstrap" procedure^{32,33} was used to determine 95% confidence limits on the estimates of the threshold (α) and slope (β) parameters of the fitted functions. These confidence limits are the error bars plotted on the figures. Predictions for the contrast thresholds for depth identification were obtained by combining the probabilities of monocular detection in each eye so as to determine the probability of simultaneous monocular detection. Full details of this probability calculation are outlined by Simmons³⁴ and Simmons and Kingdom.¹⁶ This detection threshold is the most appropriate for comparison with contrast thresholds for stereoscopic judgments because, unlike binocular detection (i.e., detection of a stimulus performed with both eyes viewing that stimulus), stereopsis requires a signal present in both eyes at the same time.^{16,34}

3. RESULTS

The results of the depth-identification experiments with vertical stimuli are shown in Fig. 2. Contrast threshold in decibels (dB) above detection is plotted against disparity in arcmin for each condition (color and luminance contrast) and each subject. Each panel of the figure incorporates two sets of data. Each set was collected as a block and spanned the different ranges of disparities: 10-60 arcmin (squares) and 60-160 arcmin (circles). Notice that the luminance contrast data are plotted with open symbols and that the color contrast data are plotted with filled symbols. The error bars are 95%confidence limits as determined by bootstrap analysis of the proportion-correct data (they are not standard errors). In these experiments "correct" was determined according to the sign of the disparity relative to fixation. Thus, for a crossed disparity the correct response was "in front" and for uncrossed disparities the correct response was "behind." The plotted data are, therefore, averaged across disparity sign. The dashed lines in Fig. 2 are the predicted depth-identification contrast thresholds (see above) based on monocular detection data.

There are a number of points to note about the disparity dependence of these thresholds. First, both color and luminance data show a threshold minimum (performance peak) at 30 or 40 arcmin of disparity. With luminance stimuli, the peak performance for both subjects is a little higher than that predicted from the monoculardetection data. With chromatic stimuli, performance never reaches the predicted level, although for FK the difference is only just over 2 dB at 40 arcmin (Fig. 2). This result has been reported previously.¹⁶ Second, both color and luminance data show a threshold maximum at disparities of 100 or 120 arcmin. Indeed, for both subjects with chromatic stimuli, the threshold performance was never obtained at 100 arcmin over the range of color contrasts tested, and so thresholds had to be estimated by extrapolation. The contrast thresholds for depth identification with both luminance and chromatic vertical Gabor stimuli thus show a cyclic dependence on disparity, with peaks and troughs in performance close to the 90-deg and 270-deg phase-display points. Note also the large error bars away from the performance peaks, which are indicative of very shallow psychometric functions.

The data obtained with horizontal stimuli show a completely different disparity dependence (see Fig. 3). Gone is the cyclic dependence on phase disparity. With the luminance horizontal Gabors, performance gradually improves with disparity until a plateau is reached at ~ 60 arcmin (although this is complicated by a range effect in the data from DS). Note that performance just overlaps with the prediction from monocular detection data, although the overlap is not as striking as it is



Fig. 2. Contrast thresholds in decibels above detection threshold for depth identification with vertically oriented stimuli, plotted as a function of stimulus disparity in arcmin for the two subjects. Open symbols, luminance contrast; filled symbols, chromatic contrasts. The different symbol shapes correspond to different stimulus-disparity ranges (i.e., the limit of the possible disparity values that could occur during a given experimental run). Squares, disparity range 10–60 arcmin; circles, disparity range 60–160 arcmin. The error bars are 95% confidence limits determined by bootstrap analysis of the proportion-correct data (see text) and are *not* standard errors. The dashed horizontal line indicates the performance to be expected if the limiting factor was simultaneous detection in each eye at the appropriate retinal eccentricity.



Fig. 3. As Fig. 2 but for horizontally oriented stimuli. Symbols are the same as in Fig. 2.

at smaller disparities with vertical stimuli as shown in Fig. 2. The data for the chromatic horizontal stimuli parallel the performance with luminance stimuli, but note the size of the gap between the chromatic and luminance contrast thresholds. Indeed, FK found it difficult to obtain threshold performance at all with horizontal chromatic stimuli, as indicated by the higher thresholds (very close to the highest contrast possible on the display) and the large error bars. Subject DS showed a somewhat better performance, but this may be accounted for by a slight change in his isoluminant point for stereopsis with stimulus orientation (see below).

The relative sizes of the difference in performance with luminance and chromatic stimuli in the two orientation conditions is illustrated in Fig. 4.

Plotted in the histogram are the ratios of best performance (i.e., lowest contrast thresholds) with luminance patterns to the best performance with chromatic patterns. The ratios are expressed as a difference in decibels and as above are based on contrast thresholds expressed in terms of multiples of detection threshold. The comparison disparities used are given in Table 1. In order to obtain equal performance, one requires that the contrast of the chromatic pattern be approximately 1.8 times the contrast of the luminance patterns when the stimuli are vertical but approximately 7 times when the stimuli are horizontal.

One possible criticism of the data presented so far is that it has been assumed that the isoluminant point as defined by minimum motion is applicable to stereopsis mechanisms. Simmons and Kingdom¹⁶ performed a control experiment in which they measured depthidentification contrast thresholds at a fixed disparity (40 arcmin) but at a range of R/(R + G) values. They found that, when vertical patterns were used, the isoluminant point as defined by minimum motion coincided with that for the highest contrast threshold for depth identification, in the sense that performance at this R/(R + G)value was not significantly better than the worst performance obtained. As mentioned above, however, one explanation of the better performance of subject DS with horizontal chromatic patterns was that the isoluminant point as defined by minimum motion was incorrect for this task. A control experiment similar to that of Simmons and Kingdom¹⁶ (Fig. 4) was thus performed, the difference being the orientation of the stimuli (i.e., horizontal) and the disparity (160 arcmin, being the disparity of peak performance with horizontal chromatic patterns for DS).

The results of this control experiment are shown in Fig. 5. Contrast thresholds for depth identification in decibels are plotted against the R/(R + G) ratio. The dashed horizontal line indicates the predicted performance level from the simultaneous-monoculardetection model. The predictions were obtained from the monocular-detection thresholds measured at each R/(R + G) ratio. Depth-identification performance was worst at an R/(R + G) ratio of 0.52. This value differed from that of minimum-motion isoluminance [R/(R + G)]= 0.57]. Nevertheless, DS, unlike FK, always found it possible to obtain threshold performance with horizontally oriented chromatic patterns.

4. **DISCUSSION**

A. Disparity Dependence of Contrast Thresholds for Depth Identification

The expected disparity dependence of contrast thresholds for depth identification in the four main experimental conditions follows from examining the nature of the stimuli. According to most current models of stereopsis there are two major sources of noise in stereoscopic discriminations, which may be termed location noise and correspondence noise.^{35,36} Location noise is thought to be caused by intrinsic noise in stereoscopic mechanisms and is most influential at low contrasts and small dispari-



Fig. 4. Histogram showing the ratio of lowest chromatic depth-identification contrast thresholds to lowest luminance depth-identification contrast thresholds, expressed as a difference in dB for the two subjects. Shaded bars, vertical stimuli, equated at 30 arcmin for DS and at 40 arcmin for FK; unshaded bars, horizontal stimuli, equated at 60 arcmin for both subjects. The thresholds used to calculate these histogram bars are shown in Table 1.

Table 1. Contrast Thresholds for Depth Identification at the Best Disparity for Two Subjects

Subject	Orientation (deg)	Type of Stimulus	Best Disparity (arcmin)	Contrast Thresholds (dB above detection)	Col/Lum ^a (dB)
 DC	v 7b	Τ	40	1 5	
DS	V	Lum	40	-1.5	_
\mathbf{DS}	V	Col	30	4.7	6.2
DS	H^{b}	Lum	140	1.2	—
DS	Н	Col	160	19.4	18.2
FK	V	Lum	40	-1.7	_
FK	V	Col	40	2.1	3.8
\mathbf{FK}	Н	Lum	100	3.3	_
FK	Н	Col	60	18.4	15.1

^aCol, color; lum, luminance.

^bV, vertical; H, horizontal.



Fig. 5. Contrast thresholds in dB above detection threshold for depth identification with horizontally oriented stimuli plotted as a function of R/(R + G) ratio, for subject DS. The error bars are again 95% confidence intervals determined by bootstrap analysis, and the dashed horizontal line indicates the performance level predicted from monocular-detection data collected at the same R/(R + G) ratio. The position of minimum-motion isoluminance is indicated by the vertical arrow.

ties. Legge and Gu have demonstrated how this type of noise can affect stereoacuity by increasing the uncertainty in the perceived depth of the stimulus.³⁵ If stereoacuity is affected by contrast, then it follows that contrast thresholds for depth identification must also be affected by disparity. Contrast thresholds should therefore increase as stimulus disparity tends toward zero. Correspondence noise refers to the depth uncertainty caused by false matches in stereoscopic stimuli. This type of noise is most troublesome at high contrasts and when there is a considerable degree of uncertainty about which feature (e.g., a bar or an edge) matches which. Correspondence noise will tend to produce spurious depth percepts in the stimulus that confuse or even completely destroy the depth percept signaled by the true stimulus disparity. Cormack et al. model this class of noise as multiple peaks in the interocular cross correlation.³⁶

These two classes of noise give rise to two generic disparity dependencies, depending on the nature of the stimulus. If the stimulus is aperiodic (e.g., a single line or bar), then there should be no correspondence noise, and consequently contrast thresholds should gradually fall as disparity increases until they reach a plateau. The level of the plateau should be determined by the stimulus detectability in the absence of other factors.^{16,34} At very large disparities, thresholds should increase again as the disparities tend toward D_{max} for stereopsis.³⁷ If, how-

ever, the stimulus is periodic (e.g., a sinusoidal grating), then both sources of noise will affect performance. One would then expect a cyclic dependence of contrast threshold for depth identification on disparity as the correspondence noise alternately gives "correct" and "incorrect" answers about the sign of the stimulus disparity. In the absence of location noise, this dependence would approximate a square wave as the depth polarity would rapidly flip when the stimulus disparity increased by half a cycle of the stimulus period. The presence of the location noise smooths out this dependence, making the rise and fall of contrast thresholds more gradual. Nevertheless, the peaks and troughs in performance should be located approximately at the 90- and 270-deg phase-disparity position, because these are the disparities associated with the least uncertainty about which features to match.³⁸

The Gabor patterns used in the experiments described here combine features of periodic and aperiodic stimuli. The underlying sinusoid, or carrier, is clearly periodic in nature, but it is confined within an aperiodic window, or envelope. Thus one might expect to see a combination of the generic aperiodic and periodic disparity dependencies for vertical stimuli. In the horizontal stimuli the carrier is orthogonal to the direction of the disparity and thus should appear to a horizontal disparity detector purely as an aperiodic stimulus.

Interestingly, the data for vertical chromatic stimuli (see Fig. 2) exhibit behavior closest to the generic periodic stimulus. Peak performance is obtained at 30 arcmin (by DS) or 40 arcmin (by FK), corresponding to the 90-deg phase-disparity condition. Worst performance in both cases is at 100 arcmin, which is close to the 270-deg phase disparity (90-arcmin absolute disparity). Note that the performance drop at 100 arcmin is total in the sense that neither subject could obtain a threshold performance level, given the range of contrasts tested. The data points plotted on the graphs were estimated by extrapolation.

The fact that this periodic dependence is found at isoluminance is not trivial. It implies that there is a chromatic stereo mechanism that can extract some feature of the isoluminant stimulus, be it a bar, an edge, or some other primitive, and match it to others on the basis of the color information. Thus red bars match red bars and green match green. This result is consistent with previous demonstrations that color information can assist the stereo correspondence process.^{3,12} A similar cyclic dependence on disparity is observed in the vertical luminance data, but there are differences in detail. The overall performance level is higher, and, more critically, depth identification is possible at detection threshold near the performance peak. The performance drop at 100 arcmin is also not total (see above), especially for subject DS. The latter observation suggests that the aperiodic envelope may be providing the subject with vertical depth information.

The horizontal luminance data (Fig. 3) exhibits almost perfect generic aperiodic behavior. Performance gradually improves with increasing disparity to reach a plateau in the region of 60 arcmin, the disparity corresponding to the standard deviation of the envelope. There is also a suggestion of a falloff at the very highest disparity measured in the data of FK. In Fig. 3 the horizontal chromatic data are similar to the luminance data in that there is a gradual improvement in performance with increasing disparity, but the most striking aspect of these results is the very low performance level. Subject FK found it impossible to obtain a threshold performance level at most disparities tested, and his threshold dependence is quite erratic. Subject DS fared rather better, but this may have been due to an inappropriate setting of the isoluminant point (see below).

B. Comparison between Horizontal and Vertical Data

The comparison histogram shown in Fig. 4 illustrates the large difference between performance with luminance and chromatic stimuli when the orientation of the carrier signal differs. The residual performance with horizontally oriented chromatic stimuli could be due to a luminance signal (i.e., an artifact) that is difficult to eliminate completely, especially at these high levels of chromatic contrast. One of the drawbacks of our technique for estimating the isoluminant point is that it does not guarantee complete elimination of luminance contrast, just a minimization of its influence. Given the high sensitivity of the luminance stereopsis mechanism, if such an artifact were only just above detection threshold it could influence performance. It is also noteworthy that, from Fig. 5, subjects DS's performance became even worse when the R/(R + G) level was changed to a slightly lower value. There is nothing necessarily strange in the isoluminant point's being different for stereopsis with vertical and horizontal patterns. As suggested above, it is likely that different mechanisms are controlling performance, and given that we are looking here at the aggregate isoluminant point of an ensemble of neurones, it is not unreasonable that, if the groups are different, they will have different isoluminant points.

In summary, the main series of data illustrates that there are two major differences between stereopsis with isoluminant and isochromatic patterns. First, when the stimuli contain contour information that is useful for stereopsis (such as vertical bars or edges), more contrast is required, relative to detection threshold, for the same performance to be achieved with isoluminant stimuli as with isochromatic stimuli. Second, if this contour information is not present, or at least is weak (as in the horizontal stimuli), then stereo performance is almost completely destroyed at isoluminance. The next question to address, then, is what may be the cause of these differences.

C. Implications for Neural Mechanisms

A hypothesis that was put forward by Simmons and Kingdom¹⁶ was that the difference between the contrast thresholds for detection and depth identification with vertically oriented isoluminant patterns may be explained by a lower density of disparity-selective mechanisms in the chromatic pathway. Yet this hypothesis cannot easily explain why this density should vary with the stimulus orientation, unless there is something radically different about the way that horizontally oriented stimuli are processed by stereoscopic mechanisms. The question thus arises as to the nature of the processing in the luminance domain of horizontally oriented patterns.

There exist two major theories about the neural encoding of disparity. In the first, which was first put forward by Barlow et al.,³⁹ the receptive fields are identical in the two eyes, except for a relative retinal displacement that endows the neurone with its disparity selectivity. In the second, championed by Freeman and colleagues,⁴⁰⁻⁴² phase differences between the filter fine structure in the left and right eyes give neurones a disparity selectivity without a relative retinal displacement in the positions of the receptive fields in the two eyes. Some authors are tending toward a compromise view that combines both types of disparity sensitivity,⁴⁰ but it nevertheless seems appropriate to consider how the horizontal disparities of horizontally oriented Gabor patterns might be detected within the context of each scheme separately and how this disparity processing might be affected at isoluminance.

1. Disparity Selectivity by Means of Relative Retinal Displacement

These units have essentially no limits on the range of disparities to which they can respond. Horizontally oriented stereoscopic stimuli would thus be processed by a mechanism with a horizontally oriented receptive field in each eye. Possibly, assuming that all early stereoscopic processing is subserved by detectors that utilize relative retinal displacement, there may be fewer of these neurones tuned to horizontal than to vertical orientations, and this difference is reflected in an even smaller proportion of these neurones that can respond at isoluminance.

2. Relative Retinal Displacement with End Stopping

The second class of mechanism that might explain performance with the horizontally oriented luminance Gabors is a stereo mechanism based on end stopping^{43,44}: in other words, a mechanism that is tuned to horizontal stimuli of a specific length and that again has a relative retinal displacement between the receptive field positions in the two eyes. Again, the question begged by this explanation is why there should be a such a large difference between performance with luminance and chromatic patterns. Possibly end stopping, being a specialized requirement, may be compromised at isoluminance.

3. Phase-Disparity Sensitivity and

Off-Orientation Looking

The standard model for disparity detection by means of phase differences between filter fine structure in the left and right eyes normally assumes that the detectors will be vertically oriented. Indeed, the prevalence of this class of neurone at vertical orientations has been taken as strong evidence that these neurones underlie stereopsis and not some other visual ability.⁴² Nevertheless, some of these neurones do have preferred orientations away from the vertical, and clearly they could contribute to stereoscopic depth perception. Indeed, Smallman and MacLeod³⁸ have emphasized that disparity detectors tuned to orientations away from the vertical can be crucially important in determining contrast thresholds for stereopsis when stimuli have a relatively broad orientation bandwidth. The question here is a slightly different one and concerns to what extent phase-disparity detectors that are capable of processing *horizontally* oriented stimuli can contribute to performance in a depthidentification task. This hypothesis was tested in the following way.

It was assumed that depth identification with horizontally oriented stimuli at large disparities was subserved by filters tuned to off-horizontal orientations. Each filter was assumed to have a receptive field matched to the Gabor stimulus, except for the orientation parameter, and was further assumed to be tuned to the horizontal disparity corresponding to a 90-deg phase difference between the fine structure in the left and right eyes.⁴⁰ There was thus a correlation between the orientation tuning and the disparity tuning of each filter, with filters closer to horizontal orientations detecting the larger disparities. The characteristic disparity d of each detector was calculated with the simple projection formula $d = 90/\cos \theta$, where d is expressed in degrees of phase of the filter spatial frequency and θ is the orientation of the filter away from the vertical.³⁸ Thus, for example, a filter with an orientation parameter of 60 deg would be responsible for detecting phase disparities of 180 deg (i.e., half a cycle), which corresponds to 60 arcmin at 0.5 cycles/deg.

An image-processing package (HIPS; Sharpimage Software) was used to generate a set of Gabor filters at a range of orientations (and therefore disparity sensitivities) that corresponded to the correct disparity tunings for the range of disparities employed in the psychophysical experiments. All other parameters of these filters, such as sensitivity amplitude and peak spatial frequency, were equal. Each filter was then convolved with a horizontal Gabor pattern generated in the same way. The filter response to this stimulus was taken to be the maximum value (i.e., largest pixel value) in the convolved output. This procedure ensured that the relative phases of the filter and the stimulus did not produce spurious changes in the size of the response. The response of each filter, calculated in this way, was normalized by dividing by the response of a horizontally oriented filter to the horizontal stimulus. This procedure therefore allowed the filter responses to be expressed as fractions of the response of a filter matched exactly to the stimulus parameters. Assuming a linear contrast-response function made it possible to calculate the contrast increment required for the off-horizontal filter to produce the same response to the horizontal stimulus as the horizontally oriented filter. Using the contrast threshold for simultaneous monocular detection as a reference point and assuming that the response thresholds for each filter were the same regardless of filter orientation made it possible to calculate depth-identification contrast thresholds for each disparity in terms of decibels above detection threshold. These

predictions are represented by the solid curve in Fig. 6. The data from Fig. 3 for both subjects are superimposed for comparison. The comparison makes clear that such off-horizontal mechanisms could underlie performance at large disparities (above, say, 60 arcmin). The lack of agreement between the prediction and the data at smaller disparities is due to the fact that the prediction takes into account only the sensitivities associated with an interocular phase difference of 90 deg and that smaller phase differences could give sensitivity to smaller disparities. A modification of the model that included these smaller phase differences and also the possibility of some form of pooled response between the 90-deg phase difference (i.e., quadrature-pair) detectors would involve a considerable number of free parameters and could easily be made to fit the data perfectly. The model presented here is intended only to provide a plausibility argument for offorientation looking and not a comprehensive explanation of the disparity dependence of the depth-identification contrast threshold with horizontally oriented luminancedefined Gabors.

The success of this model suggests that off-orientation looking may be responsible for the high level of performance with horizontally oriented luminance patterns. It is not clear, however, why there should be a change in performance at isoluminance. One would expect similar proportions of chromatically sensitive neurones at all orientations, assuming that these phase-disparity detectors, or some form of hybrid that includes positional displacements as well,⁴⁵ subserve stereoscopic performance at all stimulus orientations.

4. Linear and Nonlinear Stereoscopic Mechanisms

A final possibility for explaining stereoscopic performance with horizontally oriented luminance patterns is motivated by recent work on the division of stereo processing between so-called linear and nonlinear filtering mechanisms.^{37,46,47} The linear mechanism of Hess and Wilcox has a front-end input from conventional linear spatial-frequency and orientation-tuned filters and is thought to underlie stereoscopic performance when the



Fig. 6. Predicted contrast thresholds for depth identification with horizontally oriented luminance stimuli calculated with the methods described in the text, for the two subjects. The solid curve represents the prediction of a model in which depth identification was subserved by matched filters whose orientations were such as to render the filters tuned to disparities corresponding to a 90-deg phase difference between the filter fine structures in the two eyes. Superimposed are the luminance data of both subjects from Fig. 3.

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disparities are small relative to the characteristic period of the filter and when there is no significant correspondence problem.⁴⁶ The nonlinear mechanism extracts the contrast energy of the stimulus by using some form of nonlinearity and is thought to underlie stereoscopic performance at larger disparities and when there is a significant correspondence problem (i.e., lots of bars under the envelope). Furthermore, the nonlinear pathway is less concerned with interocular correlation than is the linear pathway and can support stereopsis even when the stimulus patterns are patches of interocularly uncorrelated noise, although the orientation contents of the noise must be similar in the two eyes.⁴⁷

According to this model, when luminance-defined Gabor stimuli are presented stereoscopically, the linear mechanism is most concerned with the disparities subtended by the light and dark bars of the carrier, whereas the nonlinear mechanism is more concerned with the disparities subtended by the envelope. It is therefore plausible that the performance deficit at isoluminance is caused by some malfunction of the nonlinear stereoscopic mechanism. One way of testing whether depth identification with our horizontal stimuli could be mediated by a nonlinear envelope-detecting mechanism is to measure performance with stimuli having similar envelope properties but whose carrier information is spatially uncorrelated between the two eyes. We therefore measured contrast thresholds for depth identification using Gabor stimuli at a disparity of 120 arcmin,⁴⁸ with three conditions of binocular presentation: in the first correlated condition identical horizontal stimuli were presented to the two eyes, as in the previous experiments; in the second, anticorrelated condition horizontal stimuli were presented to both eyes but with a phase difference of 180 deg between them such that there was negative interocular correlation; in the third, mixed-orientation condition stimuli of different orientations (horizontal and vertical) were presented to both eyes. The intention behind these experiments was to remove depth cues for mechanisms that relied on perfect interocular correlation, which include all the mechanisms discussed above with the exception of the nonlinear mechanism. Similar experiments are referred to in a chapter by Tyler.⁴⁹

The results of this control experiment are presented in Fig. 7. It is clear from this figure that there is little difference in contrast thresholds for depth identification among the three conditions. It would therefore appear that, at least at large disparities, depth identification with our horizontal stimuli could be mediated by a nonlinear envelope-detecting mechanism.

These results appear to raise problems for some theories of nonlinear stereoscopic processing. Wilcox and Hess⁴⁷ found that they could not perform stereoscopic depth discriminations with mixed-orientation stimuli that were similar to those employed here except that the patterns were envelopes of spatially filtered oriented noise rather than Gabor patterns. Tyler⁴⁹ reported experiments in which consistent stereoscopic depth was obtained with mixed-orientation stimuli, although these were orthogonally oriented obliques rather than horizontals and verticals. A further complication is that subjects reported that the depth percept associated with the mixed-orientation patterns used in the current study, as opposed to the correlated and anticorrelated horizontals, was less secure. In particular, uncrossed disparities were reported to be much less salient in the mixedorientation case, although subjects had no difficulty in performing the discrimination, and we are certain that the subjects were responding to depth and not performing some sort of utrocular discrimination (see Section 2). There are other differences between stereoscopic performance with horizontally oriented Gabor patterns and the pure-envelope stimuli of Wilcox and Hess. For example, stereoacuity with horizontally oriented Gabor stimuli depends on contrast,⁵⁰ whereas that for Gaussian-windowed noise does not.⁵¹ Also, stereoacuity is better if the horizontally oriented contents of the Gaussian envelope are correlated, as opposed to uncorrelated.⁵¹ Possibly these differences are caused by differences in experimental procedures and stimulus configurations. Nevertheless, the results from this study do indicate that a nonlinear stereoscopic mechanism is sensitive enough to explain the relatively low contrast thresholds for depth identification obtained with horizontally oriented luminance stimuli, but it appears that this mechanism is compromised at isoluminance.

5. Summary

Taken together, the above discussions suggest that there are a variety of mechanisms at work in the visual system



Fig. 7. Contrast thresholds for depth identification for the two subjects under three conditions: interocularly correlated horizontal stimuli; interocularly anticorrelated, i.e., opposite-phase horizontal stimuli (positive sine phase in one eye, negative sine phase in the other); and different orientations in each eye (horizontal in one eye, vertical in the other). Contrast thresholds are given in dB above detection threshold. The error bars are 95% confidence limits as determined by bootstrap analysis (see text).

that can process the stereoscopic depth of horizontally oriented luminance-defined Gabor patterns. Yet none of them seems to be able to process the depth as well if the pattern is chromatically defined.

D. Relevance to Previous Experiments on Stereopsis at Isoluminance

As suggested by Hess and Wilcox⁴⁶ and Wilcox and Hess,⁴⁷ one possible role of the nonlinear stereo mechanism is to take over responsibility for stereoscopic depth perception when the information coming from linear mechanisms is unreliable or ambiguous. This situation is particularly apparent in random-dot stereograms, where even in a bandpass-filtered representation of the stimulus there are a number of false matches for any given spatial primitive (be it zero crossing, peak, or whatever). It would appear from the various demonstrations of stereopsis with interocular correlations in contrast modulation but not in luminance modulation that in this situation luminance mechanisms can take advantage of similarities in contrast modulation between the two eyes. This would assist in the solution of the correspondence problem without one's having to resort necessarily to information at other spatial scales, as in many computational models of stereo matching.⁵²⁻⁵⁴ Such a mechanism would be particularly crucial to chromatic stereo mechanisms, because the range of scales available to the chromatic visual system is limited.55

These results therefore suggest a new explanation for the various failures of stereopsis at isoluminance. It appears that the chromatic stereo mechanism has two handicaps that are likely to reduce depth perception in random-dot stereograms when viewed at isoluminance. First, even if the disparities are small relative to the spatial-frequency content of the patterns, high color contrast is required for good performance to be obtained. Second, if the disparities are larger, one mechanism that would be capable of disambiguating the false matches presented is not available, possibly confusing and weakening the resultant depth percept.

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REFERENCES

- M. S. Livingstone and D. H. Hubel, "Psychophysical evidence for separate channels for the perception of form, color, movement, and depth," J. Neurosci. 7, 3416-3468 (1987).
- C. Lu and D. H. Fender, "The interaction of color and luminance in stereoscopic vision," Invest. Ophthalmol. 11, 482-489 (1972).
- V. S. Ramachandran, V. M. Rao, S. Sriram, and T. R. Vidyasagar, "The role of colour perception and 'pattern' recognition in stereopsis," Vision Res. 13, 505-509 (1973).
- V. S. Ramachandran, V. M. Rao, and T. R. Vidyasagar, "The role of contours in stereopsis," Nature (London) 242, 412-414 (1973).

- J. P. Comerford, "Stereopsis with chromatic contours," Vision Res. 14, 975–982 (1974).
- R. L. Gregory, "Vision with isoluminant colour contrast:
 A projection technique and observations," Perception 6, 113-119 (1977).
- C. M. M. de Weert, "Colour contours and stereopsis," Vision Res. 19, 555-564 (1979).
- 8. P. W. Russell, "Chromatic input to stereopsis," Vision Res. 19, 831-834 (1979).
- C. M. M. de Weert and K. J. Sadza, in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983) pp. 553-562.
- D. L. Grinberg and D. R. Williams, "Stereopsis with chromatic signals from the blue-sensitive mechanism," Vision Res. 25, 531-537 (1985).
- E. P. Osuobeni and D. J. O'Leary, "Chromatic and luminance difference contribution to stereopsis," Am. J. Opt. Physiol. Optics 63, 970-977 (1986).
- J. R. Jordan, W. S. Geisler, and A. C. Bovik, "Color as a source of information in the stereo correspondence process," Vision Res. **30**, 1955-1970 (1990).
- C. W. Tyler and P. Cavanagh, "Purely chromatic perception of motion in depth: two eyes as sensitive as one," Percept. Psychophys. 49, 53-61 (1991).
- E. P. Osuobeni, "Effect of chromatic aberration on isoluminance stereothreshold," Optom. Vis. Sci. 68, 552-555 (1991).
- L. V. Scharff and W. S. Geisler, "Stereopsis at isoluminance in the absence of chromatic aberrations," J. Opt. Soc. Am. A 9, 868-876 (1992).
- D. R. Simmons and F. A. A. Kingdom, "Contrast thresholds for stereoscopic depth identification with isoluminant and isochromatic stimuli," Vision Res. 34, 2971–2982 (1994).
- C. W. Tyler, "A stereoscopic view of visual processing streams," Vision Res. 30, 1877-1895 (1990).
- P. H. Schiller, N. K. Logothetis, and E. R. Charles, "Parallel pathways in the visual system: their role in perception at isoluminance," Neuropsychologia 29, 433-441 (1991).
- W. S. Geisler, "Sequential ideal-observer analysis of visual discrimination," Psychol. Rev. 96, 267-314 (1989).
- D. T. Lindsay and D. Y. Teller, "Motion at isoluminance: discrimination/detection ratios for moving isoluminant gratings," Vision Res. 30, 1751-1761 (1990).
- K. T. Mullen and J. C. Boulton, "Absence of smooth motion perception in colour vision," Vision Res. 32, 483–488 (1992).
- J. Palmer, L. A. Mobley, and D. Y. Teller, "Motion at isoluminance: discrimination/detection ratios and the summation of luminance and chromatic signals," J. Opt. Soc. Am. A 10, 1353-1362 (1993).
- A. B. Metha, A. J. Vingrys, and D. R. Badcock, "Detection and discrimination of moving stimuli: the effects of color, luminance, and eccentricity," J. Opt. Soc. Am. A 11, 1697-1709 (1994).
- 24. K. Boothroyd and R. Blake, "Stereopsis from disparity of complex grating patterns," Vision Res. 24, 1205-1222 (1984).
- H. S. Smallman and S. P. McKee, "A contrast ratio constraint on stereo matching," Invest. Ophthalmol. Vis. Sci. Suppl. 36, 230 (1995).
- 26. The low luminance will have resulted in large pupils and thus increased effects of chromatic aberration. However, the low spatial frequency of the stimulus should have kept these effects to a minimum. See Ref. 15 for a detailed discussion of the size and significance of chromatic-aberration artifacts in stereo experiments.
- J. D. Moreland, "Spectral sensitivity measured by motion photometry," Doc. Ophthalmol. Proc. Ser. 33, 61-66 (1982).
- S. M. Anstis and P. Cavanagh, "A minimum motion technique for judging equiluminance," in *Colour Vision: Physi*ology and Psychophysics, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983), pp. 155-166.
- 29. In the detection task the stimulus could appear randomly in one of two intervals, so the subject was uncertain as to which interval contained the stimulus. Uncertainty of this type is known to affect detection thresholds [see D. M. Green and J. A. Swets, *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966), and D. G. Pelli, "Uncertainty ex-

plains many aspects of visual contrast detection and discrimination," J. Opt. Soc. Am. A **2**, 1508–1532 (1985)]. We were concerned that, if only a single presentation interval was used for the depth-identification task, the reduced uncertainty might artificially enhance performance in the depth task relative to the detection task. Although there is also uncertainty about the disparity sign in the depth experiments, there is no evidence that this depth uncertainty can be strictly regarded as orthogonal in the manner formally required for an uncertainty condition.

- 30. Binocular-detection thresholds were measured concurrently for three reasons: (1) binocular trials interleaved with monocular trials were found to reduce the possible rivalry generated by having solely monocular trials; (2) a concurrent study of binocular summation was being performed; and (3) the level of binocular summation can provide some information on the amount of neural summation expected in the depth-identification task (although it is difficult to make a quantitative estimate of this summation).
- A. B. Watson, "Probability summation over time," Vision Res. 19, 515–522 (1979).
- L. T. Maloney, "Confidence intervals for the parameters of psychometric functions," Percept. Psychophys. 37, 286–298 (1990).
- D. H. Foster and W. F. Bischof, "Thresholds from psychometric functions: superiority of bootstrap to incremental and probit variance estimators," Psychol. Bull. 109, 152-159 (1991).
- D. R. Simmons, "Spatiotemporal properties of stereoscopic mechanisms," Ph.D. thesis (University of Oxford, Oxford, UK, 1992).
- G. E. Legge and Y. Gu, "Stereopsis and contrast," Vision Res. 29, 989–1004 (1989).
- L. K. Cormack, S. B. Stevenson, and C. M. Schor, "Interocular correlation, luminance contrast and cyclopean processing," Vision Res. 31, 2195–2207 (1991).
- 37. L. M. Wilcox and R. F. Hess, " D_{max} for stereopsis depends on size, not spatial frequency content," Vision Res. 35, 1061-1070 (1995).
- H. S. Smallman and D. I. A. MacLeod, "A size-disparity correlation in stereopsis at contrast threshold," J. Opt. Soc. Am. A 11,2169-2183 (1994).
- H. B. Barlow, C. Blakemore, and J. D. Pettigrew, "The neural mechanism of binocular depth discrimination," J. Physoil. (London) 193, 327-342 (1967).
- R. D. Freeman and I. Ohzawa, "On the neurophysiological organization of binocular vision," Vision Res. 30, 1661-1676 (1990).
- 41. I. Ohzawa, G. C. DeAngelis, and R. D. Freeman, "Stereoscopic depth discrimination in the visual cortex: neu-

rons ideally suited as disparity detectors," Science **249**, 1037–1041 (1990).

- 42. G. C. DeAngelis, I. Ohzawa, and R. D. Freeman, "Depth is encoded in the visual cortex by a specialized receptive field structure," Nature (London) **352**, 156–159 (1991).
- R. Maske, S. Yamane, and P. O. Bishop, "End-stopped cells and binocular depth discrimination in the striate cortex of cats," Proc. R. Soc. London Ser. B 299, 257–276 (1986).
- A. Dobbins, S. W. Zucker, and M. S. Cynader, "Endstopping and curvature," Vision Res. 29, 1372–1387 (1989).
- L. D. Jacobsen, J. P. Gaska, and D. A. Pollen, "Phase, displacement and hybrid models for disparity coding," Invest. Ophthalmol. Vis. Sci. Suppl. 34, 908 (1993).
- R. F. Hess and L. M. Wilcox, "Linear and non-linear filtering in stereopsis," Vision Res. 34, 2431–2438 (1994).
- 47. L. M. Wilcox and R. F. Hess, "Is the site of non-linear filtering in stereopsis before or after binocular combination?" Invest. Ophthalmol. Vis. Sci. Suppl. 35, 1086 (1994).
- 48. At this disparity the stimulus appeared diplopic.
- C. W. Tyler, "Cyclopean riches: cooperativity, neurontropy, hysteresis, stereoattention, hyperglobality, and hypercyclopean processes in random-dot stereopsis," in *Early Vision* and Beyond, T. V. Papathomas, C. Chubb, A. Gorea, and E. Kowler, eds. (MIT Press, Cambridge Mass., 1995) pp. 6–15.
- 50. F. A. A. Kingdom and D. R. Simmons, "Stereoacuity and colour contrast," Vision Res. (to be published).
- L. M. Wilcox, McGill Vision Research, Department of Ophthamology, Montreal, Quebec, Canada 3A 1A1; (personal communication, January 1995).
- D. Marr and T. Poggio, "A computational theory of human stereo vision," Proc. R. Soc. London Ser. B 204, 301-328 (1979).
- J. E. W. Mayhew and J. P. Frisby, "Psychophysical and computational studies towards a theory of human stereopsis," Artif. Intell. 17, 346-349 (1981).
- D. G. Jones and J. Malik, "Computational framework for determining stereo correspondence from a set of linear spatial filters," Image and Vision Compu. 10, 107–119 (1992).
- K. T. Mullen, "The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings," J. Physiol. (London) 359, 381-409 (1985).
- D. R. Simmons and F. A. A. Kingdom, "Differences between stereopsis with isoluminant and isochromatic stimuli," presented at the 1994 OSA Annual Meeting, Dallas, Texas, October 2-7, 1994.
- D. R. Simmons and F. A. A. Kingdom, "What causes the degradation in stereopsis at isoluminance?" Invest. Ophthalmol. Vis. Sci. Suppl. 36, 664 (1995).