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Differences between Stereopsis, Interocular Correlation and Binocularity

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In normal human subjects, evoked potentials in response to depth reversing two-color dynamic random-dot stereograms disappeared or were greatly reduced at equiluminance, whereas responses to shifts between patterns that were correlated and anticorrelated (for the two eyes) were, for most subjects, actually larger at equiluminance than at non-equiluminance. Responses were only slightly diminished at equiluminance to similar texture-shifting patterns that were identical to the two eyes. These results suggest that a significant fraction of cells with input from both eyes can respond to correlation/anticorrelation shifts, yet are not involved in stereopsis. Also, binocular rivalry may gate the responses of these binocular-nonstereoscopic units.

Stereopsis Equiluminance Binocularity

INTRODUCTION

Random-dot correlograms (Tyler & Julesz, 1976; Julesz *et al.*, 1980) are patterns in which the images presented to the two eyes shift between having corresponding elements identical for the two eyes and having corresponding elements either of opposite contrast (anticorrelated) or a random mixture of opposite and identical contrasts (uncorrelated). Such stimuli have been used for years to study stereopsis in both humans and animals (Julesz *et al.*, 1980; Miezin *et al.*, 1981; Poggio *et al.*, 1985, 1988), even though it is not clear that such patterns selectively stimulate only stereoscopic mechanisms. Indeed, in monkeys many cells that respond to shifts between correlation and uncorrelation are not disparity tuned (Poggio *et al.*, 1988).

In an earlier study on the effects of varying color and luminance contrast in red/green stereograms (Livingstone & Hubel, 1987), we had noticed that at equiluminance the depth disappeared, but the disparate region still looked different from the surrounding non-disparate region, and had a shimmering quality. This suggests that there might be features that distinguish between true stereopsis, on the one hand, and other binocular mechanisms, on the other. I therefore wanted to explore differences between stereopsis, binocularity and interocular correlation by recording evoked potentials to color-contrast dynamic random-dot stereograms and correlograms.

METHODS

Stimuli were generated on a Silicon Graphics Indigo XZ 4000, a fast color workstation capable of stereo displays. The monitor runs at a 120 Hz refresh rate, and can be used with CrystalEyes (Stereographics) liquid crystal display goggles, which alternately block the left and the right eye at 60 Hz, to present different stimuli to each eye. According to the manufacturer, the difference in transmittance between the open and closed phases of the goggles is 1000:1, but with our goggles the transmittance of the open and closed phases, as measured with a photocell, differed only by a factor of 25. Because other factors, such as phosphor persistence or lags in the rise or fall time of the lenses might also contribute to cross-talk between the signals to the two eyes, I measured the effective separation directly. Using the system's stereo mode, two bright bars were generated on the monitor, each programmed to be "seen" by only one eye; then the luminance of each bar was measured through each goggle lens, while the goggles were active (that is, switching between eyes at 60 Hz). This way of measuring cross-talk takes into consideration any contribution by phosphor persistence or lags in the rise and fall time of the goggle lenses, as well as leakage during the closed phase. By this measurement, the stereo goggles effectively attenuated luminance by 0.5 log units for the appropriate eye and by 1.8 log units to the other eye. Thus each eye sees 5% of the other eye's signal. To find out how large a physiological effect this cross-talk might

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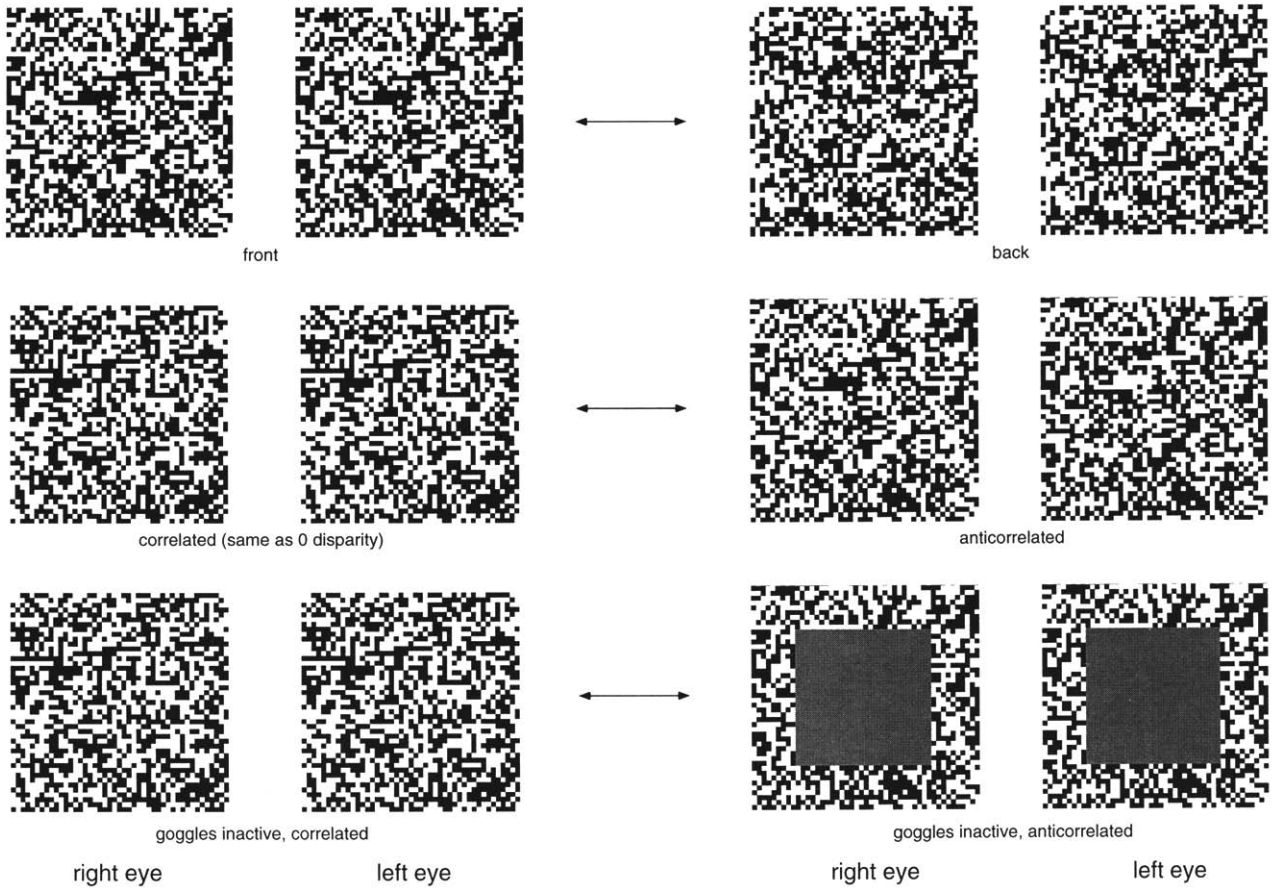

FIGURE 1. Diagram of the stimuli used in the evoked potential experiments, using black and white to represent red and green. The images are shown for crossed fusing. The stereo-pairs on the left show the stimulus configuration for the first 500 msec of each evoked potential record, and the pairs on the right show the configuration for the second 500 msec of each record.

have. I measured evoked responses to the correlation/uncorrelation stimulus viewed monocularly. This stimulus should maximize any contribution from cross-talk. Under this condition a very faint haze appeared and disappeared over the central square at 1 Hz, but the evoked potential (for three sets of 400 1 sec epochs) was no larger than baseline (which is described below). For one of the control stimuli used in this study the goggles were inactive, which left both lenses open continuously; to make the average luminance attenuation the same as when the goggles were active, 0.3 log unit neutral density filters were put over the lenses.

To generate random-dot stereograms, first, a large table of pseudo random 1 and 0 values was created, then each display used another random number to choose where in the table to start gathering values for the dots. The central 18 × 18 deg in the left eye could be given any one of the following patterns: (1) offset in position to the left or right compared to the pattern in the right eye, (2) completely unrelated to the pattern in the right eye (uncorrelated), (3) the exact opposite in contrast to the right eye (anticorrelated).

For the evoked potential studies the monitor was positioned 0.5 m in front of the subject. The random-dot stimulus covered an area of the visual field 30 × 30 deg, and the patterns were 46 × 46 squares (so each square was 40 min arc); each square was assigned to be one or the other color, with the two colors having equal

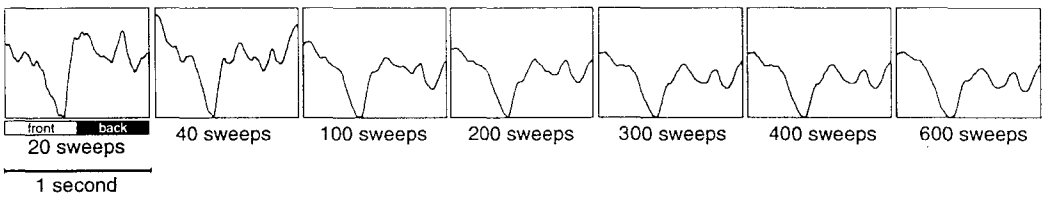

FIGURE 2. Buildup of the evoked potential for subject ML in response to the dynamic random-dot pattern diagrammed in the top row of Fig. 1, with the depth of the central square alternating between ±40 min disparity at 1 Hz. Vertical scale = 6 μV; horizontal scale = 1 sec. The number of 1 sec epochs averaged to give each record are indicated. The first record shows how the stimulus configurations of Fig. 1 correspond to the evoked potential records.

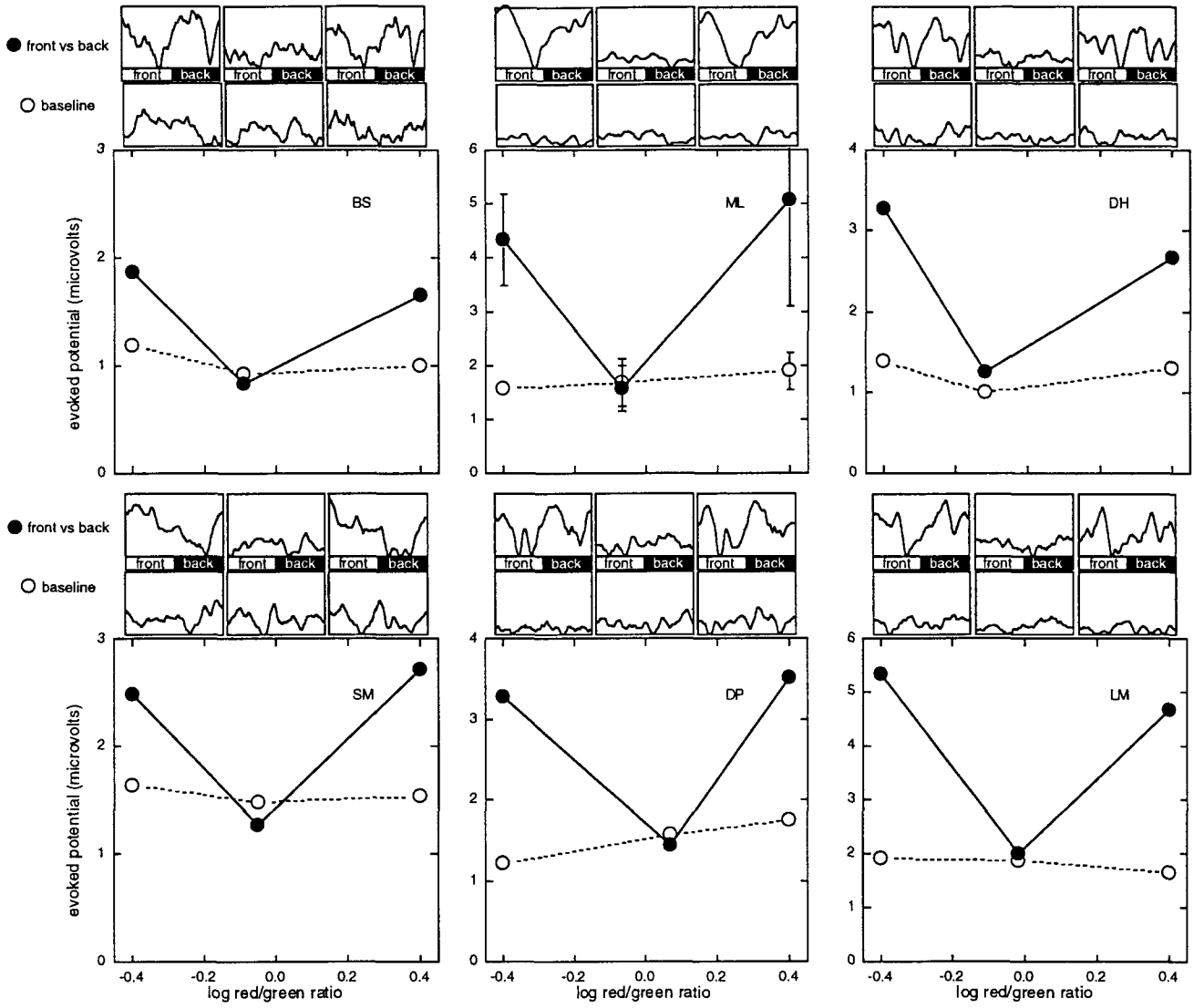

FIGURE 3. Evoked potentials to depth reversing stimuli compared to baseline EEG for six subjects. Each record is the average of 200 1 sec epochs. The filled circles, which indicate the size of the upper set of evoked potential records, represent responses to the dynamic random-dot pattern diagrammed in the top row of Fig. 1, with the depth of the central square alternating between ±40 min disparity at 1 Hz. The open circles show the size of the lower set of evoked potentials, which are the same number of epochs averaged in response to the same kind of dynamic random dots, but with the patterns continuously correlated in the two eyes, so that only the dynamic 15 Hz random-dot changes were present, with no 1 Hz Cyclopean component. Of each set of evoked potentials, the left corresponds to the stimulus with the red darker than the green; the middle to the equiluminant stimulus; and the right to the stimulus with red brighter than the green. The size of the evoked potential was measured as the difference between the maximum and minimum voltages on the averaged record. The horizontal axis for the evoked potential records is 1 sec. For each subject (except ML) the vertical scale for the evoked potential records is the same as the maximum voltage shown on the vertical scale of the graph below them. 0 on the abscissa of each graph is the photometric equiluminance point. For subject ML, five sets of each series of variables were run on separate days. The graph shows the average size of the evoked potential for the five measurements, ± standard deviation. Above the graph are shown the averaged evoked potentials for the 1000 epochs (vertical scale = 3 μV). (The evoked potentials are smaller than the corresponding points on the graph because the points on the graph represent the mean size of five 200-sweep averaged potentials while the evoked potential shown was generated by averaging all 1000 sweeps together.)

probabilities. Except as noted, the random-dot pattern changed at a rate of 15 Hz; that is, each random checkerboard pattern had a duration of 66.7 msec. This flicker of the checks produced, in all the evoked potential records, a strong 15 Hz signal, which was filtered out using a simple rolling average. A rolling average of size n, in this case 67 msec, was created by replacing each entry in a list by the average of the entry and its $n-1$ nearest neighbours. Each entry was thus replaced by the average of itself and 33 1 msec bins on either side. In one experiment the random-dot pattern changed at a rate of 4 Hz (each pattern had a duration of 250 msec).

Three different stimuli were used for the evoked potential study: (1) the background remained at zero disparity, and a central 18 × 18 deg square alternated between +40 and −40 min of disparity (or + and −8 min for the experiment shown in Fig. 6) at a frequency of 1 Hz (Fig. 1, top); (2) the central square alternated

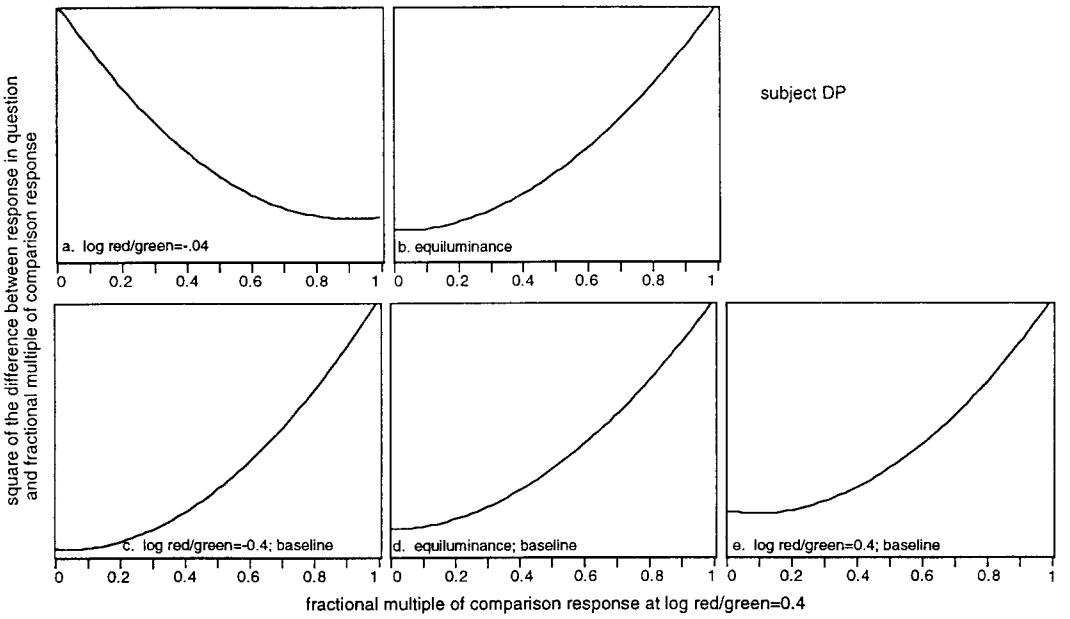

FIGURE 4. Graphs for subject DP showing the values of the sum of the squares of the differences between fractional multiples (K varies from 0 to 1 at intervals of 0.0156) of the response at log red/green = 0.4 and the other responses. Before calculating the differences between records, for each response, 0 on the ordinate was set to the arithmetic average of all 1000 of the values in the response. The vertical scale is linear, and its height is simply the maximum value obtained for each series. In panel (a) the sum of the squares of the difference between the response at log red/green = -0.4 and K times the response at log red/green = 0.4 shows a minimum at $K = 0.9$, indicating a strong similarity between the two responses, as can be seen by inspection of Fig. 3. The sum of the squares of the differences between K times the response at log red/green = 0.4 and the response at equiluminance gives a minimum at $K = 0$ (b). The baseline response at log red/green = -0.4 gives a minimum at $K = 0.036$ (c); the baseline response at equiluminance gives a minimum at $K = 0$ (d); and the baseline response at 0.4 gives a minimum at $K = 0.42$ (e).

between being correlated in the two eyes and being anticorrelated (Fig. 1, middle); (3) the goggles were inactivated and the stimulus consisted of the same correlation/anticorrelation shifts (Fig. 1, bottom). These stimulus alternations were presented continuously, at an alternation rate of 1 Hz, so the recordings represent steady-state responses. To establish the baseline EEG activity in response to the dynamic random-dot patterns, the same number of 1 sec epochs were recorded while the dynamic patterns were correlated in the two eyes, with no 1 Hz component (in practice the depth was set to zero).

Luminances were measured with a Pritchard spot photometer. During testing the room was lit with dim overhead tungsten lights, so that the background luminance of the monitor, with all phosphors set to zero, was 3×10^{-3} candelas/m^2. The stimuli were dynamic random-checked patterns of green and red squares (using simply the red and green phosphors). The luminance of the green squares was kept constant at 0.5 cd/m^2 and the brightness of the red checks varied over the full range of the monitor's capacity for the variation of the red gun.

The subjects were volunteers from our department. Six potential subjects were rejected because they had small evoked potentials to depth reversing stimuli (less than 2 μV for the first 40 sweeps) or because they could not see stereoscopic depth. Three of the participating subjects (students) were paid. The participating subjects all had corrected-to-normal acuity and were capable of seeing stereoscopic depth, in that they could see the square defined only by disparity differences in the dynamic random-dot stereogram and described it as jumping from in front of the background to behind it. I did not measure subjects' stereoacuity, except for myself, for whom more extensive comparisons were made. As the disparity of the dynamic stereogram shifted back and forth between ± 40 min disparity, each subject was asked to vary the red phosphor value and to report when the square and/or the sensation of depth disappeared. The range of red settings over which the sensation of depth disappeared was recorded. The subjects were asked to make this determination five times, and the average of the midpoints of each of the ranges was used as the subject's equiluminance point. Each subject was very consistent in choosing a particular red/green ratio.

Evoked potentials were recorded using 10 mm diameter gold-plated EEG electrodes attached to the scalp with conductive paste. The recording electrode was placed at O_Z (90% of the distance from nasion to inion), which is directly over V1, and the reference electrode was attached to the left earlobe. A ground electrode was placed at C_Z [50% of the distance from nasion to inion (Jasper, 1958)]. The signals were amplified 20,000 times and filtered with a low frequency cut-off of 0.3 Hz and a high frequency cut-off of 100 Hz. Responses were sampled every millisecond. Subjects were instructed to try to maintain fixation at or near the center of the display. Except for subject ML, all the stimulus conditions were tested at a single sitting; for each stimulus condition 200 1 sec response intervals were averaged (except in the experiment shown in Fig. 6, in which sets of five 200 sec responses were averaged). In all cases, the stimuli were presented alternating continuously at 1 Hz for 200 sec,

with rest periods between each 200 sec set. As shown in Fig. 2, 200 averages are adequate to determine the response amplitude and wave form. The size of the evoked potential was taken as the excursion between the highest and lowest voltage values for the averaged, filtered record.

Stereoacuity in subject ML was measured by the method of adjustment (Graham, 1965). The subject sat 6 m from the monitor. The stimulus consisted of three parallel bars, all 1 × 0.1 deg, with the flanking bars separated by 0.5 deg. The subject turned a knob to vary the position of the central bar so that it appeared to lie in the same plane as the two flanking bars. Acuity was taken as the standard deviation for 15 trials at each color ratio, in seconds of arc. For this experiment, the subject was the author, but the disparity settings could not be seen by the subject, and were recorded by an associate who did not know the hypothesis being tested; no feedback was given. The different color ratios were presented in randomly interleaved blocks of 15 trials.

RESULTS

Responses to disparity shifts

For the first series of experiments the stimulus was a dynamic random-dot stereogram in which a central square alternated between ±40 min disparity. Subjects were first asked to find a red setting at which the depth sensation was minimum. Of the first colleagues who volunteered for the experiment, most could find a red setting at which the sensation of depth pulsation seemed to completely disappear. Two, DH and SM, could not find such a setting. These subjects said that at red settings at which the square (which at non-equiluminance jumped from front to back) disappeared, the stimulus continued to have a vague central region (one of them called it a "Gaussian blob") that bounced in and out in depth. The location of this pulsating blob within the central square moved around with their gaze. There are at least two possible explanations for this residual stereopsis: it could arise from differences between equiluminance ratios between the fovea and periphery resulting from macular pigmentation (Cavanagh *et al.*, 1987; Livingstone & Hubel, 1987). A second possibility was suggested by Patrick Cavanagh: that the blob may arise from chromatic aberration, or luminance artifacts at the edges of the checks, and that a signal of such high spatial frequency may be discernible only near the fovea. It is of course possible that this depth sensation represents true chromostereopsis, but that would not be consistent with its being restricted to the central 1 deg of the visual field.

For all the subjects tested, including DH and SM, the evoked responses recorded in response to shifts between positive and negative disparities were larger than baseline when the red was brighter or darker than the green, but decreased to baseline amplitude at the subjectively determined equiluminance point (Fig. 3). The reproducibility of this result is shown for one subject (the author) for whom measurements were made on five separate days (all variables of each set were tested each day). The shape of the evoked response to depth reversal varied from subject to subject, but for any one subject, the responses at the two luminance extremes were similar.

Although the amplitude of the depth reversal responses

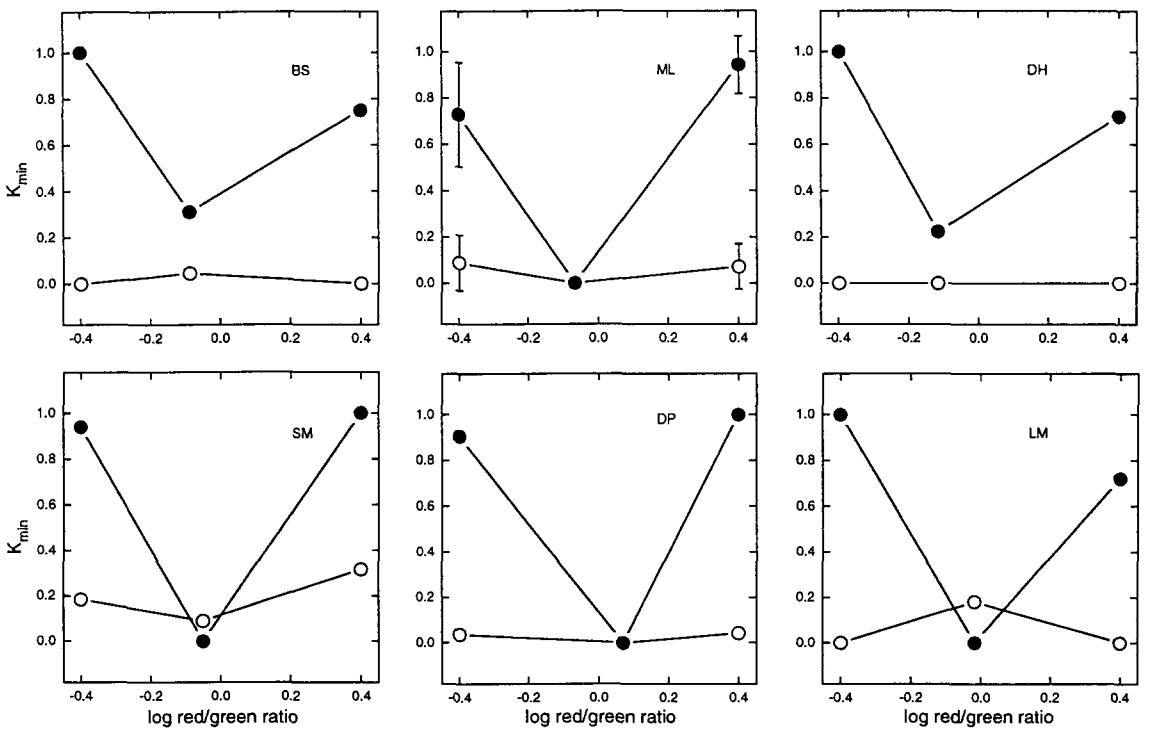

FIGURE 5. Graphs showing the values of K giving a minimum in the sum of the squares of the difference between K times the largest response and the other responses at each color ratio (K_{min}). For subject ML, K_{min} were calculated for each of the five series of measurements and then averaged. Error bars indicate standard deviations.

at equiluminance were no larger than the baseline responses, the shape of the waveforms resembled the responses at non-equiluminance for three of the subjects (BS, DH and DP, and perhaps SM), suggesting that there really was some response. I therefore wanted to see whether it could be shown, for any of the subjects, that the depth reversing response at equiluminance was a scaled-down version of the depth reversing response at non-equiluminance. A calculation was used that directly compares two waveforms of different amplitudes—a least squares fit was calculated between the smaller of the two and a series of fractional multiples of the larger.

If Ψ_t is the larger of two waveforms and V_t is the smaller, we calculate a sum, S

$$S = \sum_{t=0\rightarrow 1} (K\Psi_t - V_t)^2$$

at each value of K from 0 to 1, at intervals of 0.0156.

For any one subject, the largest response (which is always one of the depth reversing responses at non-equiluminance) is compared to all of his or her other responses. Essentially this asks what fractional multiple (K) of the larger waveform gives the best fit (minimizes the sum of the squares) to the smaller waveform. Thus for identical waves, S is minimum at $K = 1$ and for completely unrelated waves, S is minimum at very small values of K. For example, for subject DP, the response at the log red/green ratio -0.4 was smaller than the response at 0.4, so the latter was used as the standard for comparison with all his other responses. Figure 4(a) shows the values of S as a function of K for the comparison between DP's response at log red/green = -0.4 and his response at 0.4. This calculation shows a minimum in the value of S at $K = 0.9$, indicating a strong similarity between the two responses, as can be seen by inspection of the waveforms in Fig. 3. A comparison between the response at red/green = 0.4 and equiluminance gives a minimum in the value of S at $K = 0$ [Fig. 4(b)]. All three depth = 0 responses also show minima at or close to $K = 0$ [Fig. 4(c,d,e)]. We define K_{min} as the value of K giving the minimum value for S. Figure 5 shows the values of K_{min} for all subjects for the depth reversing stimuli and for the baseline responses. For two subjects the depth reversing response at equiluminance was larger than 0. The value of K_{min} at equiluminance for BS was 0.31 and for DH was 0.22.

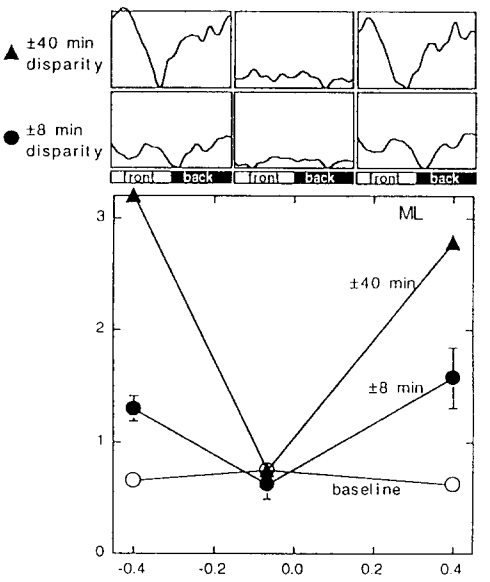

FIGURE 6. Evoked potentials for subject ML in response to large and small depth reversals. Stimuli subtended 30 deg of visual angle and were 46 × 46 checks. A central 18 × 18 deg region oscillated at 1 Hz between ±8 or ±40 min disparity (data for the larger disparity are also shown in Fig. 3). For ±8 min disparity, at each color ratio three sets of 1000 1 sec epochs were recorded in interleaved sets of 200 1 sec epochs. The filled circles on the graph show the average size for the three sets of measurements; error bars indicate the standard deviation. The open circles show the size of the average of 1000 1 sec epochs of baseline response at each color ratio; the filled triangles show the size of the average of 1000 1 sec epochs of the ±40 min disparity shift. The records above the graph show the average evoked potentials for the two different disparity shifts at each color ratio (1000 1 sec epochs were averaged together for each color ratio for the ±40 min disparity shift and 3000 epochs were averaged together for each color ratio for the ±8 min disparity shift); vertical scale = 3 μV.

That is, for these two subjects there did seem to be some similarity between the response at equiluminance and the response at non-equiluminance. Because the baseline was not always 0, however, we needed to compare these values to the average K_{min} for the baseline EEG. The average value of K_{min} for all of the baselines compared to the same subject's maximum depth reversing response (all six subjects at all color ratios) was 0.058 and the standard deviation was 0.092. Thus only for subject BS was the equiluminance response more than 2 standard deviations larger than the average value for the baseline.

Tyler (1990) has suggested that the magno and parvo subdivisions of the visual system carry information about different ranges of disparity—that small disparities (<20 min) are carried by the parvo system and larger disparities (>20 min) by the magno system. I therefore tested the effects of equiluminance on responses to disparity shifts in these two ranges by measuring responses to 16 and 80 min disparity shifts.* Because the responses to the smaller disparity shift were smaller, more responses were averaged. It is not obvious why a larger disparity shift should give a larger response, but this has been observed previously in humans and in squirrel monkeys (Norcia *et al.*, 1985; Livingstone *et al.*, 1995). Figure 6 shows that for subject ML responses to the 16 min shift (between ±8 min disparity) were smaller

*To make a 16 min display shift, but still have 40 min-wide checks, the central region had to be shifted by a fraction of a check width. This necessitated the presence of a small monocular cue. The visibility of this cue was minimized by having the central square shifted 8 min arc (2 pixels) in the same direction alternately in each eye's image. Thus, using both eyes, there was a continuously visible 2-pixel-wide border on the left edge of the central square (also the checks on the right edge alternated between being 100% and 80% as wide as the rest, but this was undetectable even under the closest scrutiny). Each eye alone saw the left border appear and disappear at 1 Hz. Evoked potentials (three sets of 1000 1 sec epochs) recorded to this stimulus viewed monocularly were no larger than baseline, indicating that this tiny monocular cue was not responsible for the responses to the depth shift.

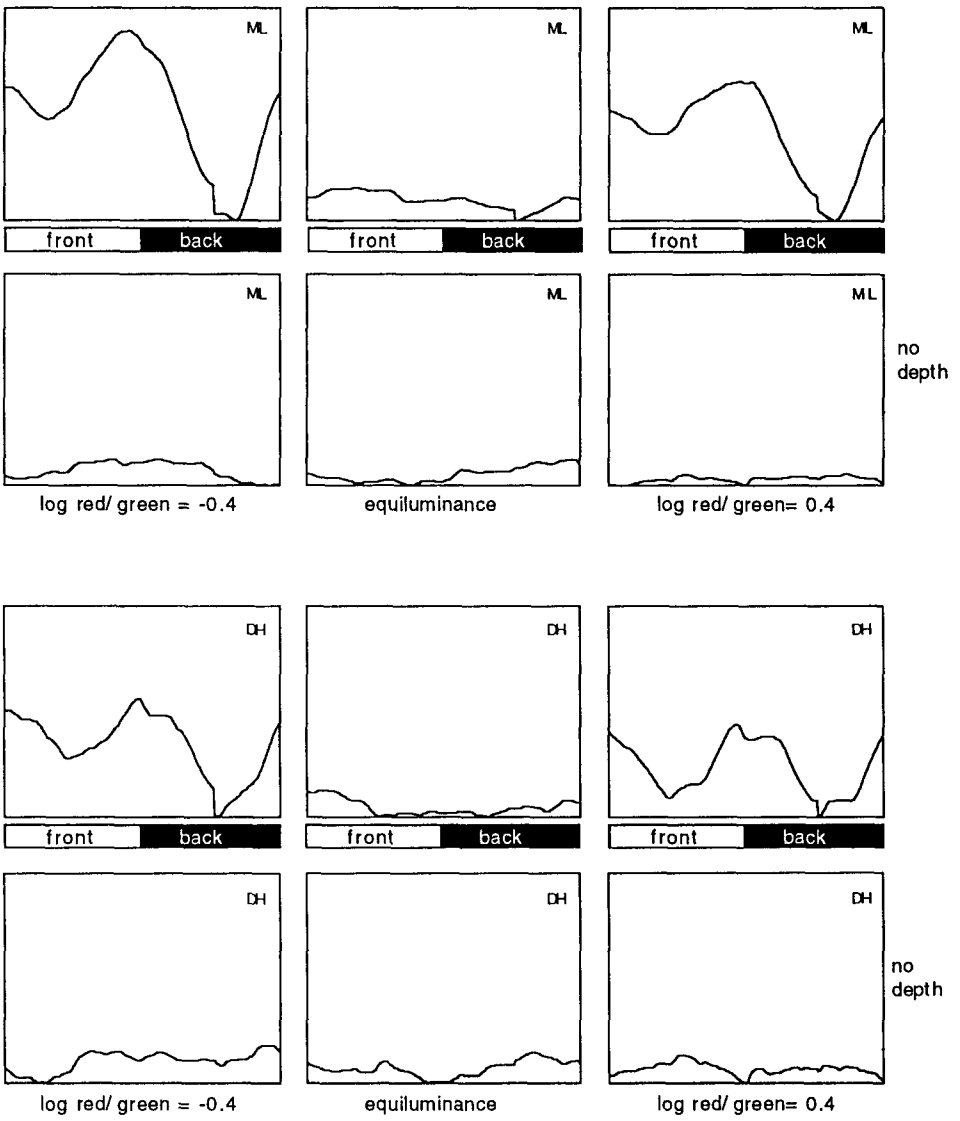

FIGURE 7. Responses of two subjects to 1 Hz alternations between ±40 min disparity, using a dynamic random dot pattern renewal rate of 4 Hz (pattern duration 250 msec). For subject ML 200 1 sec intervals were averaged for each record, and for subject DH 100 1 sec intervals were averaged to give each record. Below each set of evoked potentials for depth reversals are baselines—averages of equivalent durations of spontaneous EEG activity in response to the dynamic random-dot pattern, with no depth alternations. For all the records shown a rolling average (of 250 msec) was used to filter out the 4 Hz component. For all records the abscissa is 1 sec; for ML the vertical scale is 3 μV; for DH the vertical scale is 2 μV.

than responses to shifts between ±40 min, but for both depths the responses fell to baseline at equiluminance. Averaged responses for the two disparity shifts are shown above the graph. The shape of the response is similar for the two different disparities, though the response may be slightly delayed for the smaller disparity.

It could be argued that the dynamic presentation of different random-dot patterns at 15 Hz might compromise perception at equiluminance, since flicker resolution is slower at equiluminance than at non-equiluminance (Ives, 1923). For several reasons, however, I think that the speed of the dynamic pattern change is not the explanation for the observed selective loss of stereopsis here. First, the contrast-reversal flicker fusion rate for the same colors measured on the same monitor under the same conditions is 15 Hz, which is equivalent to double the rate used in these experiments.* Second, in the evoked response records a 15 Hz component was filtered out to reveal more clearly the 1 Hz responses; in the unfiltered records this component was only slightly reduced at equiluminance, compared to non-equiluminance. Third, as described below, the response to correlation/uncorrelation shifts increases at equiluminance, and this response presumably requires discrimination of the same dynamic random-dot pattern. Nevertheless, to be certain that the speed of the random-dot pattern renewal rate was not too high, I tested two subjects using a dynamic random-dot renewal

*Because one cycle of a contrast-reversal stimulus comprises one presentation of each of two colors or contrasts, a contrast reversal stimulus has a duty cycle of two stimulus durations, whereas the rate for a dynamic random-dot pattern has a duty cycle of a single pattern duration.

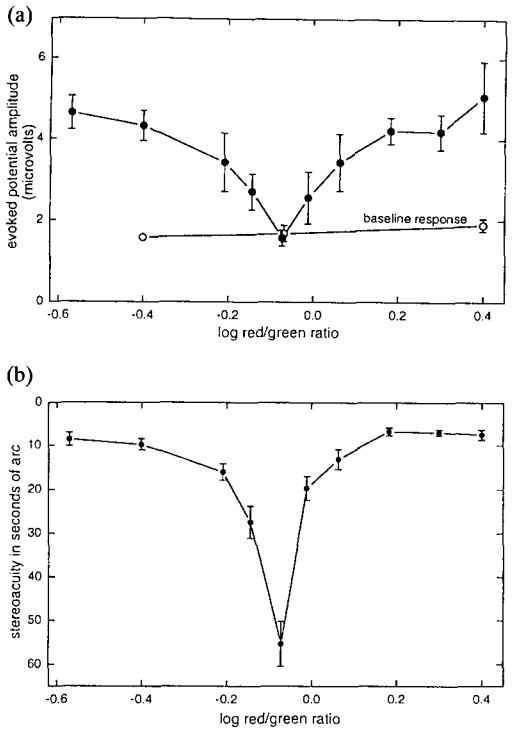

FIGURE 8. Comparison of evoked potential and stereoacuity as a function of luminance and color contrast for subject ML. Evoked potentials (a) were recorded in response to a 1 Hz oscillation between ±40 min disparity of a central region of a dynamic random-dot stereogram, as diagrammed in Fig. 1, top. The baseline response was to the same dynamic random-dot stimulus but continuously correlated (with no 1 Hz Cyclopean component). In a single sitting 200 1 sec epochs were measured for each red/green ratio; in each set the color ratios were randomly interleaved. The size of each evoked potential was taken as the excursion from the highest to the lowest voltage value of the averaged record. Averaged evoked potentials for each red/green ratio were measured on five different days; each point on the graph represents the mean value for the five sets of 200 1 sec averaged potentials for each color ratio. Error bars indicate the standard error of this mean. Stereoacuity was measured as the standard deviation, in seconds of arc, of 15 attempts by the subject to set the depth of a central bar to be the same as two flanking bars. Each point on the graph indicates the average of five such sets of measurements, and the error bars indicate the standard error of the mean.

rate of 4 Hz (pattern duration of 250 msec). As shown in Fig. 7, both subjects still showed a large decrease in their evoked potentials to depth reversals at equiluminance, even using this slower stimulus.

Stereoacuity

For one subject (ML) evoked potentials to depth reversals were measured at several different red/green ratios, and the results were compared to the same subject's stereoacuity at the same red/green ratios (Fig. 8). Both functions are similar in shape and show a sharp minimum at equiluminance. For the stereoacuity test a central bar was moved in depth (disparity) between two flanking bars; the task was to adjust the disparity until the central bar appeared to lie in the same plane as the flanking bars. At equiluminance the central bar no longer seemed to move in and out of the plane of the monitor, but at large disparities the images for the two eyes could be seen to fuse and unfuse; one tended to "cheat" at equiluminance by using this convergence and divergence to estimate the matched positions for the two eyes. Thus the measured stereoacuity at equiluminance of 1 min arc is probably an overestimate.

Correlation/anticorrelation and texture shifts

I looked at evoked responses to another stimulus that has been used extensively in stereopsis research: shifts between correlated and anticorrelated dynamic random-dot patterns (Fig. 1, middle). Evoked responses to this stimulus were quite different from the responses to the depth reversing stimuli: rather than showing a large decrease in response at equiluminance, most of the subjects tested showed an increased response at equiluminance (Fig. 9). This elevation in response at equiluminance was statistically significant ($P = 0.0014$, paired t-test). For comparison, evoked potentials were recorded to a texture-shift, in which the same correlation/anticorrelation stimulus was used, but with the stereo goggles inactive and a 0.3 log unit neutral density filter added to equate the luminance attenuation (Fig. 1, bottom). Responses at equiluminance to this non-stereo shift were only slightly smaller (15% smaller on average) than at the two luminance contrasts used.

DISCUSSION

Is stereopsis diminished or unaffected at equiluminance?

The reduction of the evoked response to depth reversing stimuli at equiluminance is consistent with reports that stereopsis is perceptually impaired at equiluminance. This study differs from previous studies on the perception of stereopsis at equiluminance in that it uses *dynamic* random-dot stereograms and in that it measures a graded physiological parameter as well as the subject's perception. Previous studies on the effect of equiluminance on stereopsis fall into four categories: (1) those that find a loss or significant decrease in stereopsis at equiluminance (Lu & Fender, 1972; Gregory, 1977; De Weert, 1979; Livingstone & Hubel, 1987), (2) those that find that color can contribute to stereopsis, but more weakly than luminance (Comerford, 1974; De Weert & Sadza, 1983; Osuobeni & O'Leary, 1986; Simmons & Kingdom, 1994), (3) those that show that color can disambiguate ambiguous stereo matches defined by luminance (Triesman, 1962; Julesz, 1971; Jordan *et al.*, 1990; Kovács & Julesz, 1992) and (4) those that find a strong contribution of color to stereopsis (Tyler & Cavanagh, 1991; Stuart *et al.*, 1992; Scharff & Geisler, 1992). This present paper would fall primarily into the first category (loss or significant decrease in stereopsis at equiluminance). Nevertheless, even though the evoked response amplitude of most subjects decreased to baseline levels, I do not want to claim that stereopsis is eliminated at equiluminance—the evoked potential of some subjects was not eliminated entirely, and two of the subjects in this study always saw some part of the stereogram moving in depth at all luminance ratios. It is possible that had I varied the color ratio around

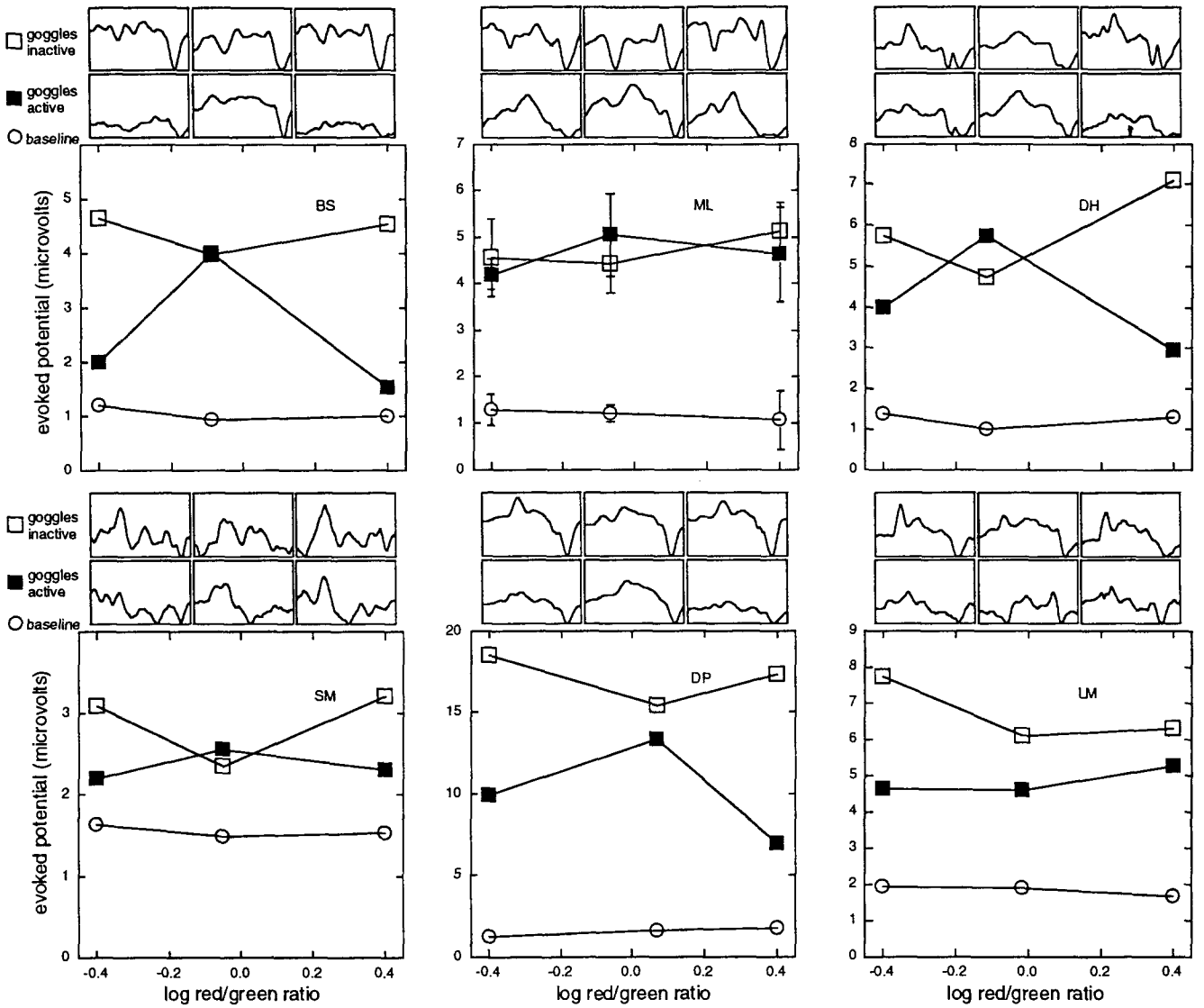

FIGURE 9. Evoked potentials for six subjects in response to correlation/anticorrelation shifts, correlation/anticorrelation shifts with goggles inactive, and a baseline stimulus. Each record is the average of 200 1 sec stimulus epochs. The solid squares, which indicate the size of the lower set of evoked potential records, represent responses to the stimulus in which the central square region of a dynamic random-dot correlogram oscillated at 1 Hz between having the patterns identical for the two eyes and having the patterns of opposite contrast in the two eyes (stimulus diagrammed in the middle row of Fig. 1). The open squares show the size of the upper set of evoked potentials, which are in response to the exact same stimulus with the stereo goggles inactivated (and a 0.3 log unit neutral density filter placed in front). The open circles show the baseline response (same as in Fig. 3) which is the dynamic random-dot pattern kept at 0 disparity (continuously correlated) with no 1 Hz signal. Of each set of evoked potentials, the left corresponds to the stimulus with the red darker than the green; the middle to the equiluminant stimulus; the right to the stimulus with red brighter than the green. In each case the size of the evoked potential was measured as the excursion between the maximum and minimum voltages on the averaged record. The horizontal axis for the evoked potential records is 1 sec. Except for subject ML, the vertical scale for the evoked potential records is the same as the maximum voltage shown on the vertical scale of the graph below them. For the graphs, 0 on the abscissa is the photopic equiluminance point. For subject ML, three sets of each series of variables were run on separate days. The graph shows the average size of the evoked potential for the three measurements, ± standard deviation. Above the graph are shown the evoked potentials for the 600 1 sec epochs averaged together (vertical scale = 6 μV). (The average evoked potentials are smaller than the corresponding points on the graph because the points on the graph represent the mean of the sizes of three 200 sweep potentials while the evoked potential shown was generated by averaging all 600 sweeps together.)

equiluminance, those subjects might have shown further decreases in their evoked response. It is also possible that the residual perception of depth at equiluminance was due to an artifactual presence of luminance-contrast information. None of the studies listed in the second category above, or this study, controlled for the possibility that macular pigmentation might make the equiluminance points for the fovea and the periphery different, thus introducing a luminance-contrast signal at all color ratios. Therefore even the second category of results (decrease but not loss of stereopsis at equiluminance) does not rule out the possibility that stereopsis requires luminance-contrast. And if we consider the possibility that an essentially color-blind system might exhibit responses to color contrast, without caring about the color itself, as has been postulated for the motion

system by Dobkins and Albright (1993), then a mere decrement, and not necessarily a loss, in stereopsis at equiluminance is entirely consistent with the idea that stereopsis is carried by a non-color-opponent system.

Now we ask whether the publications in the third and fourth categories are inconsistent with the idea that stereopsis is carried primarily by a non-color-opponent system. I suspect that the studies in the third category, those that find that color can disambiguate ambiguous stereo matches of luminance-defined items, may be describing a special aspect of stereopsis, one that reflects some kind of top-down influence of one system on another and that could well use color information. I will discuss this again in connection with the role of color in motion processing. Lastly, the three studies that seem to show that color plays a very strong role in stereopsis may, on close examination, not be too difficult to reconcile with these results. The paper by Stuart *et al.* (1992) looks at the effect of adding color and luminance noise to luminance and color-contrast random-dot stereograms. The strong role for color found in this study may reflect its ability to disambiguate potential matches for luminance-defined edges, so I would place this paper in category 3. (That is, in their stereograms the two kinds of checks always differed in luminance; which luminance-defined checks would be chosen to match in the two eyes could be driven by either luminance or color similarity. This is analogous to the situation described for the balloons below.) Tyler and Cavanagh (1991) also find that color can provide a strong input to stereopsis, but their comparison is to movement perception, which, as discussed below, probably also is carried by a largely color-blind system. I think it is quite possible that the percepts of both stereopsis and motion can be derived from color information, but I think it is the decrement in performance at equiluminance under conditions under which some other visual task is much less affected that is the signature of a magno-dominated performance. Scharff and Geisler (1992) found that, of three subjects, one showed a large decrease in stereo-contrast sensitivity at equiluminance and two did not. In their study stereo-contrast sensitivity was measured at the photometric equiluminance point and in 5% contrast intervals on either side of that point (these steps are larger than the luminance-ratio steps in Fig. 7 of this paper), so they might easily have missed the equiluminance point of some of their subjects (note, for example, how much the experimentally determined equiluminance points for our subjects differ from the photometric equiluminance point).

Magno or parvo?

The question of whether behavior at equiluminance can shed light on the subdivisions of the visual pathway involved is a vexed one. Work from this laboratory has indicated that responses from cells in the magnocellular layers of the macaque lateral geniculate nucleus show greatly diminished responses at the human equiluminance point. Though color-coded cells in the parvocellular layers also show decreased responses at particular color ratios, these ratios are not at the human equiluminance point, and moreover they vary from cell to cell within the parvocellular layers (Schiller & Colby, 1983; Hubel & Livingstone, 1990). Most of the physiological studies done so far find that cells in the magno system show much larger response decrements at equiluminance than cells in the parvo system (Derrington *et al.*, 1984; Lee *et al.*, 1988; Hubel & Livingstone, 1990; see however, Logothetis *et al.*, 1990).

A comparison with motion perception may shed some light on the role of color in stereopsis. Motion perception is dramatically slowed at equiluminance (Ramachandran & Gregory, 1978; Cavanagh *et al.*, 1984), but it is still perceived (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985) and direction can be discriminated (Sato, 1988; Mullen & Boulton, 1989). Gegenfurtner *et al.*, (1994) used color contrast gratings to compare responses of cells in monkey MT to monkey perceptual performance and concluded that the monkey's perceptual performance at equiluminance was better than could be accounted for by the responses of MT cells, which show greatly decreased responses at equiluminance, though they still respond and retain directional selectivity (Saito *et al.*, 1989; Dobkins & Albright, 1994). Dobkins and Albright (1993), Gorea and Papathomas (1989) and Morgan and Ingle (1994) also addressed this paradox by looking at ambiguous motion stimuli, in which motion can be seen in either of two directions depending on which elements are chosen to correspond from one instant in time to the next. They found that under quite particular conditions color itself, and not just color borders, can contribute to motion perception—by disambiguating ambiguous motion correspondence. Taken together, all these results can be interpreted as showing that there is a part of the visual system selectively concerned with motion processing (the magno-MT pathway), and that this system is comparatively insensitive to color but does have access to color information in two ways. (1) The system is responsive to color-contrast borders, without being sensitive to the sign of the colors making up the borders. This sensitivity could arise from the physiologically observed "frequency doubling" response described by Schiller and Colby (1983); (2) some other pathway in the visual system, which is sensitive to color, can also contribute to motion perception. Its contribution might be some kind of a top-down influence, as it seems to be brought out most effectively in situations in which luminance-contrast information provides the motion signal, but where the direction of the motion is ambiguous, and color information is used to select between otherwise equally likely corresponding elements. Color may indeed be even more effective than luminance contrast for this tagging purpose: imagine a cluster of balloons, some filled with helium and some filled with helium plus air; if the balloons were different colors, and all the red ones had more helium and tended to rise faster than the other colors, it would be easy to see what was happening. It

would be more difficult to figure out what was happening if all the balloons were different shades of gray, and the faster rising ones were the lighter shades of gray. It would be still more difficult if the balloons were all different colors and brightnesses, and the fastest ones were just the lighter colors.

The situation may be similar for stereopsis; most of the studies that report a significant contribution of color to stereopsis use situations in which color is used to disambiguate ambiguous or rivalrous luminance-defined stereoscopic matches (Triesman, 1962; Julesz, 1971; Jordan *et al.*, 1990; Kovács & Julesz, 1992; Stuart *et al.*, 1992). Thus for both motion and stereopsis the primary stream may be broadband, but color may contribute, or appear to contribute, in three ways: (1) color-opponent input may be used to modify or influence the broadband responses, particularly under circumstances of ambiguous matches; (2) the system may be responsive to color-contrast borders without caring about the sign of the contrast; (3) lastly, for some subjects, macular pigment and/or high spatial frequency artifacts may make it very difficult to achieve equiluminance across enough of the visual field to test global stereopsis or motion perception.

The LGN lesion studies of Schiller *et al.* (1990) may seem to contradict the hypothesis that stereopsis, like motion, is primarily carried by a broadband system. They found loss of stereopsis after parvocellular lesions and no deficits after lesions to the magnocellular layers, suggesting that the parvocellular system provides the major contribution to stereopsis. This result is difficult to reconcile with reports of decreased stereopsis at equiluminance and with physiological observations that cells with disparity tuning are most often found in magno-stream areas—layer 4B of V1 (Livingstone & Hubel, 1984; Poggio, 1995); the thick stripes of V2 (DeYoe & VanEssen, 1985; Hubel & Livingstone, 1987); and in MT (Maunsell & Van Essen, 1983; Roy *et al.* 1992; Bradley *et al.* 1995). The results of the present study may help resolve this apparent conflict. The stimuli that Schiller *et al.* (1990) used were such that the monkeys could have distinguished the target on the basis of correlation/uncorrelation signals. Had the monkey been required to distinguish positive from negative disparities, magnocellular-lesion effects might have been seen.

Tyler (1990), on the other hand, has suggested that both the magno and parvo subdivisions of the visual system carry information about disparity, but cover different ranges of disparity—that small disparities are carried by the parvo system and larger disparities by the magno system. One might therefore expect different effects at equiluminance for these different disparity ranges. Yet, as shown in Fig. 6, evoked potentials for 16 arc min disparity reversals show the same kind of decrease at equiluminance, as do evoked potentials for 80 arc min shifts. Also, the diminution at equiluminance was strikingly similar for ML's stereoaccuracy and her disparity-evoked potentials, even though her stereo acuity was as high as 10 sec arc (and should thus involve Tyler's "fine" disparity system) and the evoked potential stimulus was a disparity shift of 80 arc min (which should involve his "coarse" system). Tyler does not regard a diminution of stereopsis at equiluminance as evidence against its being a parvocellular function because he suggests that both the parvo and magno systems should be compromised at equiluminance. Ingling and Drum (1973), have argued that a typical parvocellular Type 1 cell can show diminished responses at equiluminance if the stimulus has a high enough spatial frequency that the center activation by one color is balanced by surround inhibition from the other color. This point of view predicts that the spatial scale of the stimulus should determine the degree of response decrement at equiluminance. Yet Figure 2 shows that responses to three stimuli with exactly the same spatial frequency content are very differently affected by equiluminance: responses to the correlation/anticorrelation shift increase, responses to the texture shift decline on average by less than 15%, while responses to the depth reversal stimulus decrease to baseline. It therefore would seem more likely that the different color-vs-luminance responsiveness described here for stereopsis and correlation/anticorrelation reflect contributions from different processing streams, rather than alternative behaviors within a single stream.

How are correlation/anticorrelation responses related to stereopsis?

The fact that evoked responses to correlation/anti-correlation shifts *increase* at equiluminance whereas responses to depth reversing stimuli *decrease* suggests that different populations of cells respond to these two stimuli. The depth reversing stimulus presumably activates disparity-selective cells. As for the correlation/anticorrelation responses, Poggio *et al.* (1988) have recorded the responses of cells in macaque areas V1 and V2 both to disparity stimuli and to correlation/anti-correlation shifts (though they do not distinguish between responses to anti- and uncorrelation). In their studies, shifts between correlation and un- or anticorrelation differentially activated three populations of cells: (1) cells preferring non-zero disparities were usually excited by uncorrelation and inhibited by correlation; (2) cells tuned to zero disparity [the Tuned Excitatory cells of Poggio and Fischer (1977)] were usually excited by correlation and inhibited by uncorrelation; (3) cells with no disparity tuning ("Flat" cells, or ordinary binocular cells) were usually excited by uncorrelation and inhibited by correlation. Thus more kinds of cells should respond to our correlation/anticorrelation shifts than to the depth reversals.

Let us assume that the large decrease in response at equiluminance to depth reversal implies that a large proportion of cells responsive to near or far disparities should similarly give decreased responses at equiluminance. The quite different effect of equiluminance on responses to correlation/anticorrelation shifts implies that correlation/anticorrelation evoked responses must be dominated by a different population of cells, one that does not show decreased responses at equiluminance.

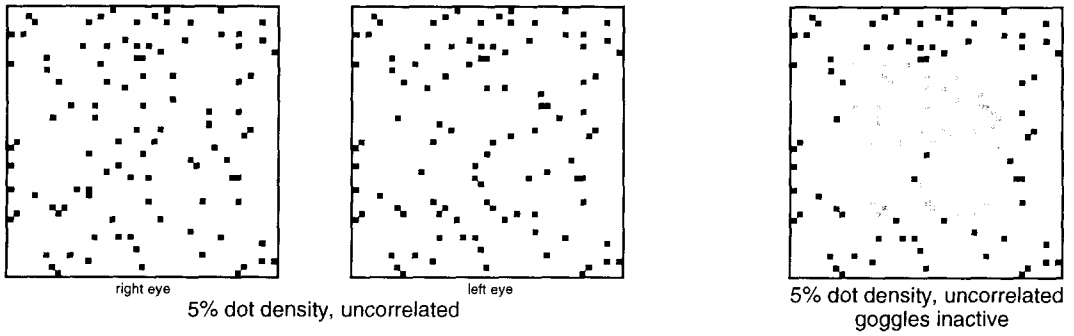

FIGURE 10. Diagram of the kind of stimuli used by Poggio *et al.* (1988). Their stimuli differed from the correlation/anticorrelation stimuli used here in having a lower dot density and in using uncorrelation not anticorrelation. The dot density used in the experiments reported here was always 50%, but Poggio *et al.* varied the dot density, and often used much lower densities. On the left is a correlogram with an uncorrelated central region (as opposed to anticorrelated). On the right is what that same correlogram would look like with the stereo goggles inactive. By comparison with Fig. 1, our correlation/anticorrelation stimulus is more potent, which may explain why only one third of their ordinary binocular cells responded to their correlation/uncorrelation stimulus.

This population could include both non-disparity-selective cells [the Flat cells of Poggio *et al.* (1988)] and disparity-selective cells. The salience of the bottom panel of Fig. 1 suggests that a large component of the response to correlation/anticorrelation could come from non-Cyclopean binocular cells, that is, cells that simply combine the inputs from the two eyes as if the goggles were inactive. If such cells exist, they would be categorized as "Flat" by Poggio *et al.*, and they might respond to the stimulus of the middle-panel of Fig. 1, just as if it showed the dramatic texture shift of the bottom panel. This speculation is consistent with the finding of Poggio *et al.* (1988) that one-third of the "Flat" cells they recorded from responded to correlation/uncorrelation shifts. Poggio *et al.* often used a much lower dot density than we did and often used uncorrelation instead of anticorrelation. Such a stimulus is illustrated in Fig. 10, along with what it would look like with the goggles inactive (which is also what it might look like to ordinary binocular units). In comparing this stimulus with our Fig. 1, our correlation/anticorrelation stimulus is more salient, which may explain why only one third of their ordinary binocular cells responded to their correlation/uncorrelation stimulus. It may be that an even higher percentage of their cells would have responded to the higher density correlation/anticorrelation stimuli used here.

The increase in the evoked response at equiluminance for the correlation/anticorrelation stimulus is intriguing. In previous studies, responses to shifts between correlation and un- or anticorrelation have been assumed to reflect stereoscopic mechanisms (Tyler & Julesz, 1976; Julesz *et al.*, 1980; Miezin *et al.*, 1981; Poggio *et al.*, 1985, 1988), yet here evoked responses to correlation/anticorrelation shifts and responses to depth reversing stimuli showed very different dependencies on luminance- vs color-contrast, suggesting that they are carried by different parts of the visual system. Perceptually, at non-equiluminance, the central square of the anticorrelated stimulus looks like a three-dimensional cloud of dots (red and green, not yellowish), but at equiluminance it looks almost identical to the same stimulus with the goggles inactivated—a homogeneous tan square. That is, at non-equiluminance the anticorrelated stimulus does seem to activate depth mechanisms, and presumably the sensation of multiple depths arises from the large number of false stereoscopic matches available. The checks in the anticorrelated region are each seen as one or the other of the two colors used, not blended in color; that is, at non-equiluminance the presence of rivalry seems to prevent the fusing of the different colored inputs to the two eyes. At equiluminance the images from the two eyes do seem to fuse—the same potential stereoscopic matches in the anticorrelated patterns are ignored, and each check is fused with its opposite, giving a homogeneous blended central square, as shown in the bottom panel of Fig. 1. Thus the stimulus appears to shift between a dynamic high spatial frequency random-dot pattern and a steady homogeneous tan of equal brightness—a dramatic shift. The increased evoked potential for this stimulus at equiluminance could then be explained if rivalry, like stereopsis, is diminished at equiluminance, revealing a salient transition—between the homogeneous steady tan and the high-contrast dynamic red and green checks. Because the evoked response to the depth reversing stimulus diminished to baseline at equiluminance, let us assume that the entire stereo system also becomes much less responsive at equiluminance. Then the fact that the evoked potential to correlation/anticorrelation increases at equiluminance suggests that that response is dominated by non-stereo-selective cells. Purely monocular cells would not see any signal at 1 Hz, but binocular cells that simply combine the inputs from the two eyes (as if the goggles were inactive) would see a dramatic 1 Hz shift between dynamic checks and a steady homogeneous tan. Since the evoked response to this same stimulus with the goggles inactive decreases slightly at equiluminance, the increase at equiluminance with the goggles active suggests that at non-equiluminance some other system might be inhibiting those ordinary binocular cells. Since the stereo system seems to be more active at non-equiluminance, it is a good candidate for providing

TABLE 1.

	Depth reversal	Texture shifts	Correlation/anticorrelation	Color
Stereopsis	Responds	No response	Responds (to false matches)	Primary input broadband
Binocular, non-stereo cells	No response	Responds	Responds (to texture shift)	Color and broadband inputs
Rivalry	?	No response	Responds (to anti-corr)	Primary input broadband

inhibition predominantly at non-equiluminance. That is, I suggest that stereo-selective (or rivalry-selective) cells modulate the response of the ordinary binocular cells, decreasing their responses under situations of binocular rivalry. This idea is consistent with what one sees: at non-equiluminance the anticorrelated checks appear to be one or the other color and do not blend, and they seem to lie in many depth planes, but at equiluminance they blend to a homogeneous flat square. Liu *et al.* (1992) have shown that at low contrasts rivalrous stimuli can fuse, which would be consistent with this idea that the responses of some binocular cells are inhibited under situations of rivalry.

Table 1 summarizes a hypothetical scheme for stereopsis, binocularity and rivalry that would explain the results and conclusions from this study. Here rivalry and stereopsis are treated separately, but it is quite possible that they are closely related functions, or that one subsumes the other. Note that although all three systems are postulated to respond to the correlation/anticorrelation stimulus, they respond for different reasons.

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