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Failure of Rivalry at Low Contrast: Evidence of a Suprathreshold Binocular Summation Process

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Presentation of different images to the two eyes normally results in a time-varying alternation between the two images (binocular rivalry). However, we find that when orthogonal gratings are viewed dichoptically at low contrast, a stable summation between the two images is perceived in the form of a dichoptic plaid. The range of perception of the dichoptic plaid depends on spatial frequency, contrast and luminance of the gratings. This phenomenon differs from the "false fusion", a fleeting summation of different images perceived only under very brief presentation of the stimuli. The observations suggest that there exists a neural process that performs a summation of dissimilar images, and that is distinct from the competitive process of suppression and binocular rivalry.

Binocular fusion Binocular rivalry Binocular summation Contrast sensitivity Spatial frequency

INTRODUCTION

Hitherto, there have been two principal combination rules for suprathreshold contours falling on the corresponding points of the two eyes (Wolfe, 1986; Blake, 1989). When the monocular images are similar or identical, a unified binocular representation is formed (binocular fusion). This new cyclopean image may not be the same as either of the monocular half images. However, if the two monocular images are very dissimilar, they tend to compete to reach consciousness. The usual percept is the rivalrous alternation of the two monocular images, between states of dominance and suppression (binocular rivalry). Both binocular fusion and binocular rivalry are nonlinear combinations of two eyes' contour information, in a sense that both processes involve some degrees of suppression. In the case of binocular fusion it is the two original images that are suppressed in favor of the combined percept. In the case of binocular rivalry one of the two original images is suppressed at any particular time independently in local regions of the visual field.

The rivalry alternation caused by two dichoptic images has been intensively studied (e.g. Helmholtz, 1896; Breese, 1899; Levelt, 1965). The temporal characteristics of binocular rivalry depend strongly on the "stimulus strength", a term used by Levelt (1965) to specify the combined effect of such stimulus parameters as luminance, contrast, density of contours and movement. One of the important conclusions was that when the stimulus strength decreases, the alternation slows down. Although this is generally true for strong stimuli (for example, stimuli of high contrast) or imbalanced stimuli (as shown by Blake, 1977), there have been no studies of the fate of the alternation when the stimulus strengths of both stimuli are simultaneously reduced to contrast threshold level. Would the alternation continue, at a progressively slower rate, until the monocular patterns fall below their own detection thresholds? Or would the alternation be replaced by a new kind of perception when the stimulus was weak but still above threshold? Our observations show the latter to be true. Under a wide range of conditions, two dissimilar monocular images can be perceived in a summative fashion that is qualitatively different from the suppressive effects in binocular fusion and binocular rivalry. When a pair of low contrast sinusoidal gratings at orthogonal orientations are shown dichoptically (one to each eye of the observer), a "dichoptic" plaid consisting of both orientations can be seen. The percept is very close to the plaid produced by the physical summation of the two gratings.

Transient perceptual combination of orthogonal gratings has been noticed by some authors who studied binocular rivalry (Abadi, 1976; Hollins, 1980). In his study of inhibitory interactions during dichoptic viewing, Abadi (1976) asked his observers to look at a suprathreshold induction grating in one eye while increasing the contrast of an orthogonal grating in the other eye from zero until "the amount of contrast entering the left (testing) eye is such that it momentarily provides a binocular patchwork field". Using orthogonal dichoptic gratings, Hollins (1980) noticed that between two exclusive visibility states in which only one

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eye's stimulus was perceived, a composite of the two eyes' stimuli could be seen. This composite could be a mosaic consisting of interspersed portions of the two targets or a blend in which intersecting contours could be seen. De Weert and Wade (1988) studied the relationship between the correlation of two eyes' microstructures (random dot patterns) and the rivalry of the macrostructures (gratings embedded in the random dot patterns). They found that when the microstructures of the two eyes were +1 correlated there was very little predominance of either monocular stimulus. Again, these authors put mixtures and composites of the two eyes' views in the same category and compared them with the exclusive visibility of either eye's stimulus. In none of these studies, however, was anything said about the completeness and stability of the combination of the two eyes' views, probably because the authors believed that when orthogonal gratings were presented to the two eyes there could only be rivalry. It could be crisp, only exclusive views of one stimulus or the other could be seen; or indistinct, a patchwork, composite or mixture could be seen and these were merely a transitory state between the two exclusive eye-dominance states. We argue that, however, even in the absence of exclusive visibility there are still two types of perception. One is the piecemeal, time-varying pattern usually seen when a pair of large dichoptic stimuli are used. The other is the state of dichoptic plaid perception; a congruent, stable fusion of the two dichoptic stimuli. The piecemeal mixture is a clear sign of rivalry in local regions of the visual field whereas the dichoptic plaid is a sign that rivalry has been overcome by a stable fusion process. These two states should therefore be carefully distinguished.

It is also well known that if a pair of dichoptic patterns are presented briefly, a fleeting summation of the two can be observed, even at very high contrast (Hering, 1920; Wolfe, 1983). A systematic study of this "false fusion" by Wolfe (1983) showed that spatial frequency and luminance of the stimulus had very little effect on the perception of plaid, whereas the timing of the stimulus was crucial: dichoptic stimuli could be fused only if presented for durations shorter than 150 msec. Wolfe (1983) interpreted this fused perception as an "abnormal" behavior of the visual system before the rivalry mechanism was activated. The dichoptic plaid phenomenon we report, however, is a stable perception which can last for as long as several minutes, as may be seen in the demonstration provided in Fig. 1. The stability of the dichoptic plaid perception depends on the stimulus parameters. Low contrast is crucial in reaching a stable dichoptic plaid percept; low luminance also helps.

Recently, Livingstone and Hubel (1987) have suggested that rivalry might disappear at high spatial frequencies. They believed that rivalry resulted from the activity of the magnocellular pathway, and that the rivalry mechanism failed with fine orthogonal gratings due to the lower spatial resolution of the magnocellular pathway. But the dichoptic plaid perception we observed can happen over a wide range of spatial frequencies and is not confined to very fine grid. So the conclusion appears to be that contrast, rather than spatial frequency, is the critical variable in achieving a nonrivalrous stable plaid perception. Even the high contrast gratings Livingstone and Hubel used to demonstrate the disappearance of rivalry were not much above detection threshold, considering the high spatial frequency. The distribution of spatial frequency components in the dichoptic stimuli is important in a sense that they determine at which contrast range the dichoptic plaid can be stably perceived. This paper will describe the stimulus conditions under which the dichoptic plaid perception can be achieved.

METHODS

The stimuli were orthogonal gratings generated by a computer and displayed on the faces of two Tektronix-608 cathode-ray tube monitors (CRT's) with P31 phosphor. A computer independently controlled the waveform, contrast and temporal modulation of the gratings presented on the two monitors. The average luminance of the stimulus was always 40 cd/m^2 whereas the grating contrast, defined by $(I_{max} - I_{min})/(I_{max} + I_{min})$, could be adjusted by the observers. Stimulus size was controlled by a set of opaque masks with circular apertures so that for all spatial frequencies there were always 6 cycles of the gratings showing in the aperture. Using a chin rest, subjects with good acuity and stereopsis looked at the gratings through a mirror haploscope. No fixation aid was used. Between stimulus presentations, a blank field with the average luminance was shown for at least 2 sec. During this period the subjects were encouraged to blink or to close their eyes to eliminate the afterimages of the previous stimulus.

In the experiments to be described we measured two types of threshold. In determining the monocular detection threshold, we showed a grating to one of the observer's eyes and a blank field of equal luminance to the other. The observer adjusted the contrast of the grating until detection threshold was reached. The procedure was repeated for the other eye, and the average of the two monocular thresholds was taken as the monocular detection threshold. In determining the binocular rivalry threshold, orthogonal gratings of the same waveform, same spatial frequency and same contrast were shown dichoptically. At the beginning of each experiment, the contrast was always low so that a dichoptic plaid could be perceived throughout the duration of the stimuli. The observer then increased the contrasts of both gratings jointly until the perception of the plaid began to break up and rivalry took over.

The first experiment concerned the duration of the dichoptic plaid perception. The observer initiated the dichoptic stimulus by pushing a button and then pushed another button when any disintegration of the plaid was noticed. The computer measured the time elapsed between the two button-pushes. The stability and the stimulus dependency (contrast and spatial frequency) of dichoptic plaid perception was well established in this

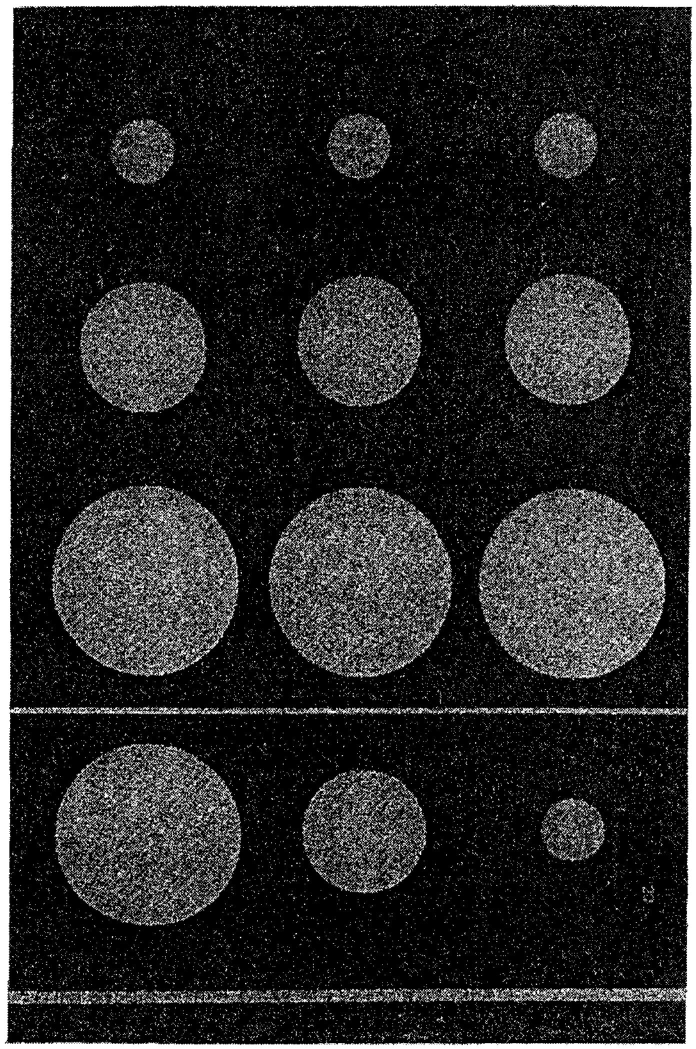

FIGURE 1. Demonstration of the dichoptic plaid phenomenon. The first three rows are three sets of dichoptic stimuli. If you cross your eyes and view the image from a distance of 1 m you can see four columns of apertures, two binocular flanked by two monocular. The middle two columns are the results of dichoptically combining the original central column with the left and the right columns. The percepts obtained in the first three rows should be similar to the representations of the three panels in the bottom row. Note, however, that one of the two combined stimuli may give a more stable plaid perception than the other if there is any uncorrected anisometropia and/or astigmatism in one eye. Because of the difficulty in reproducing the stimuli, the contrasts of the gratings are higher than the optimal values and the aperture sizes are larger than required for a long-lasting dichoptic plaid. As a result, the perceived plaid may collapse several seconds after the apertures are fused, and refusion will be required to restore it. A weak luster percept may also be seen in the second and the third rows. Note that strong eye dominance or astigmatism tend to disfavor dichoptic plaid perception.

experiment. However, it is not feasible to use very long durations for parametric experiments. So, in the following four experiments, which explored the spatial and temporal properties of the dichoptic plaid perception, we used presentations of moderate durations.

One of the authors (L.L.) and two other observers (J.G. and B.L.) participated in the first five quantitative experiments. To test the consistency of the dichoptic plaid phenomenon in a larger population, a survey was conducted in which ten second-year optometry students were randomly chosen to serve as observers. All the observers either had normal vision or wore appropriate refractive corrections.

RESULTS

Experiment I. The duration of dichoptic plaid perception

To characterize the temporal stability of dichoptic plaid perception, we first measured the duration of the dichoptic plaid percept at different contrast levels. Gratings of identical spatial frequency and contrast but orthogonal orientations were used as stimuli. By pushing a button the observer initiated a stimulus with abrupt onset and offset. At the onset of the stimulus, a plaid could always be seen. The observer then pushed another button when any disintegration of the plaid was noticed.

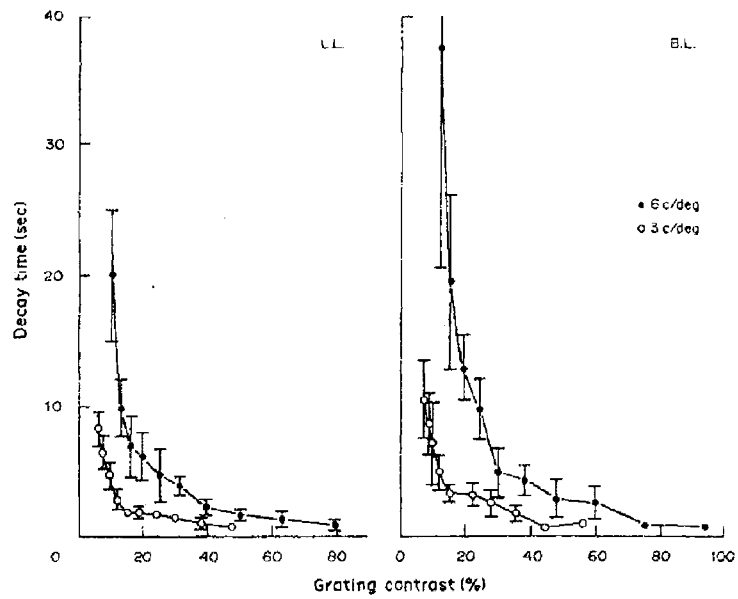

FIGURE 2. Dichoptic plaid decay time in seconds plotted against contrast for two subjects. Decay time refers to the time elapsed between the onset of the orthogonal gratings and the disintegration of any part of the dichoptic plaid. Plots are given for two spatial frequencies of the orthogonal gratings. Experimental conditions were similar to that in Fig. 4 except that the contrast was fixed in each trial and the duration for which the subject could see a dichoptic plaid was recorded. Datum points are the mean of ten measurements with standard deviations denoted by error bars.

The computer measured the time elapsed between the two button-pushes. Ten measurements were taken for each contrast level at two spatial frequencies (Fig. 2). When the contrast was high, the dichoptic plaid percept was fleeting and lasted for only about 200 msec, consistent with Wolfe's (1983) observations. As contrast was reduced, the duration of stable plaid increased gradually, but there is a knee in the function at about 15% for 3 c/deg gratings below which the duration of the dichoptic plaid increased by as much as two orders of magnitude. The higher spatial frequency grating produced a longer lasting dichoptic plaid perception at all contrast levels.

Experiment II. Effect of luminance

The effect of luminance on dichoptic plaid perception was then examined. Monocular detection thresholds and binocular rivalry thresholds for 5 c/deg orthogonal sinusoidal gratings were taken at three luminance levels: 40, 4 and 0.4 cd/m^2. The mean luminance was changed by adding neutral density filters in front of both apertures. The duration of the stimulus was 500 msec, again with abrupt onset and offset. The results from two observers are shown in Fig. 3. Unlike "abnormal fusion", in which mean luminance level has been shown to have no effect (Wolfe, 1983), dichoptic plaid perception was facilitated by lower luminance, in that higher contrast could be tolerated before rivalry ensued. Note that the binocular rivalry thresholds changed in proportion to monocular detection thresholds as the mean luminance was changed, so that the range of dichoptic plaid perception was always 1.2–1.5 log units above detection threshold.

Experiment III. Effect of temporal profile

To determine whether dichoptic plaid perception was caused by an abrupt stimulus onset, we compared two temporal modulations of the contrast; a sharp-edged temporal square wave with a duration of 1 sec and a trapezoidal temporal wave with a flat top of 1 sec, ramped on and off for 1 sec each. Horizontal and vertical dichoptic gratings of 5 c/deg were the spatial stimuli. The binocular rivalry thresholds under these temporal modulation conditions was taken with an adjustment procedure. The results were that the dichoptic plaid percept was equal or even stronger for the gradual onset condition. For observer L.L. the binocular rivalry thresholds were the same for the two temporal modulations (16%), but for observer J.G. gradual change in contrast gave better plaid perception (26% for the square wave and 56% for the trapezoidal wave). These results indicate that dichoptic plaid perception was not a transient phenomenon triggered by the onset of the stimulus. This distinguishes dichoptic plaid perception from false fusion, which depends crucially on the transience of the stimuli.

Experiment IV. Effect of spatial frequency

The effect of spatial frequency on dichoptic plaid perception was studied with abrupt presentations of 500 msec duration. Monocular detection thresholds and binocular rivalry thresholds for a range of spatial frequencies were compared in Fig. 4. Above the monocular detection threshold and before binocular rivalry started, there was a contrast region in which a stable dichoptic plaid could be seen for the whole 500 msec duration of

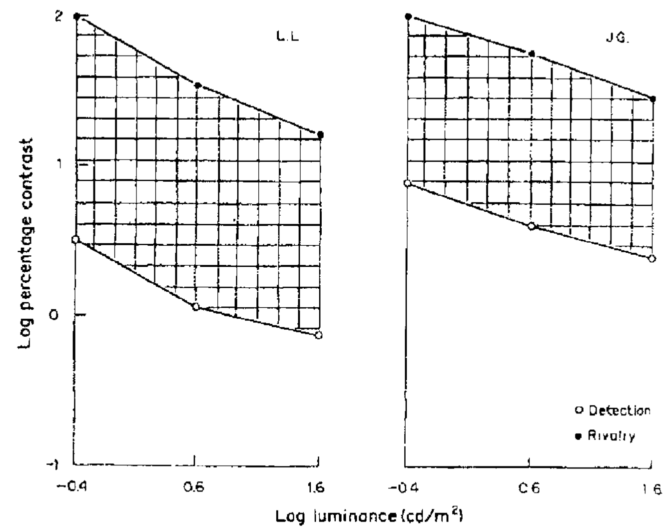

FIGURE 3. Monocular detection thresholds (open circles) and binocular rivalry thresholds (solid circles) at mean luminance of 40, 4 and 0.4 cd/m². Neutral density filters were used in front of both apertures to produce different luminance levels. The stimuli were 5 c/deg sinusoidal gratings. Circular apertures in a dark field were used to expose six cycles of the gratings for each spatial frequency. Target contrast was stepped on and off with a duration of 500 msec. The contrast was adjusted by the observer to meet each criterion. Open circles refer to binocular thresholds, where the criterion was to see a plaid filling the whole aperture throughout the duration of the stimulus. The average standard deviation was 1.3%. The hatched areas indicate the contrast ranges where the dichoptic plaid was seen continuously for 500 msec. Between two stimulus presentations, two blank fields were shown and the observers were encouraged to blink or to close their eyes during this period to eliminate afterimages from the previous stimulus. The balance of the two eyes' stimuli was important. Lower mean luminance increases both detection threshold and rivalry threshold.

the stimulus. The range of this percept depended on spatial frequency; with 1 c/deg orthogonal gratings, constant plaids could be seen only below 10% contrast, whereas with 6 c/deg gratings, the limit went to about 80%. The gap between monocular and binocular thresholds increased towards higher spatial frequency, suggesting some extra contribution of higher frequencies to dichoptic plaid perception. The perceived plaid pattern was neither a mosaic of pieces from the two monocular gratings nor one grating hovering transparently above the other. It appeared as a solid combination of the two orthogonal gratings with darker blobs at the intersections of dark bars and lighter blobs at the intersections of light bars. This was more obvious with

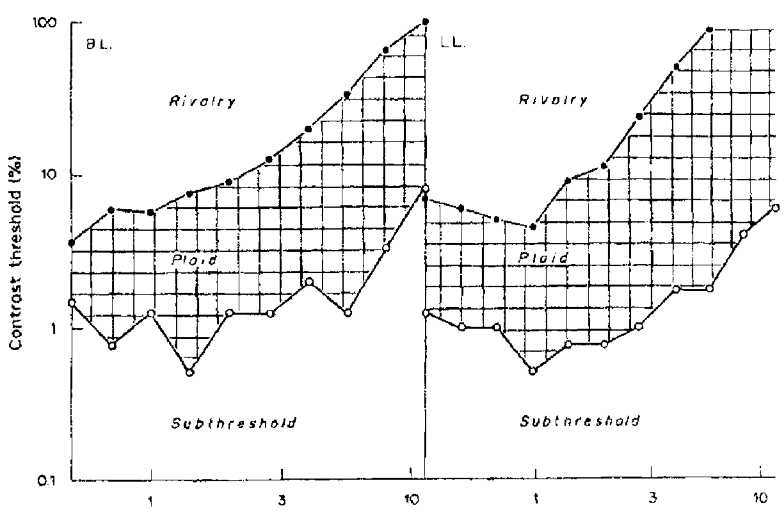

FIGURE 4. Contrast thresholds plotted against spatial frequency for two subjects. Other details as in Fig. 3, except that mean luminance was 40 cd/m². Note that the dichoptic plaid was visible for a similar range at all spatial frequencies.

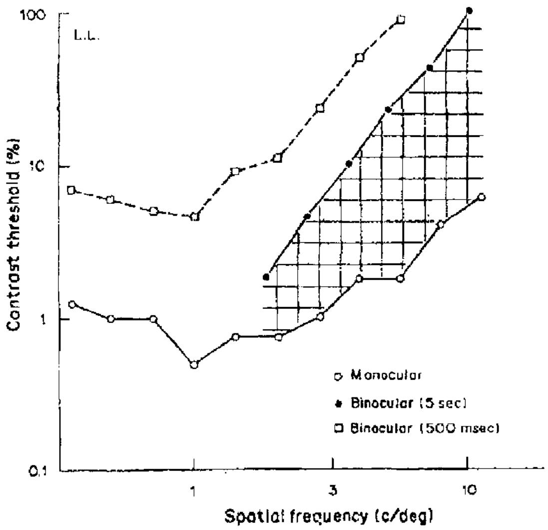

FIGURE 5. Contrast thresholds plotted against spatial frequency for subject L.L. The experimental conditions were the same as those in Fig. 4 except that the stimulus duration was 5 sec. Solid circles refer to binocular thresholds obtained with 5 sec duration whereas open symbols are monocular and binocular thresholds obtained with a 500 msec duration. Hatched area indicates the contrast ranges where a dichoptic plaid could be seen for the full 5 sec. With 5 sec duration, binocular thresholds for spatial frequencies lower than 2 c/deg could not be determined even with detection threshold contrasts (see text).

moderate spatial frequencies, where the blobs forming the intersections became more visible than the linear bars of either grating. There was also a faint impression of binocular luster in these stimuli, but it appeared uniform across the field of the perceived plaid.

To measure the properties of the dichoptic plaid percept for longer times, binocular rivalry thresholds were also taken for 5 sec stimulus durations for one observer (Fig. 5). There was a uniform drop of binocular rivalry thresholds for long duration stimuli at higher spatial frequency, but there was still an extensive region within which stable plaid perception was maintained for this extended duration. At low spatial frequency, however, plaid perception was not sustained even with near-threshold contrast; the two gratings would start alternating in a gradual way shortly after the onset of the stimulus.

Experiment V. Effect of spatial waveform

Dichoptic plaid perception was also sensitive to the spatial pattern of the stimulus. In the third experiment we compared binocular rivalry thresholds at different stages of synthesizing a square wave from its Fourier components. The fundamental frequency of the square wave was 0.5 c/deg. Three cycles were shown in the window for all gratings. The duration of the stimulus was 2 sec. The results from two observers are shown in Fig. 6. The fundamental alone (a sine wave of 0.5 c/deg) did not give stable dichoptic plaid perception for the 2 sec presentation. When the first one or two higher harmonics were added to it, however, the dichoptic plaid composed of the compound gratings could last the whole stimulus duration. As more harmonics were added, the dichoptic plaid percept could tolerate correspondingly higher contrasts. Full square wave gratings elicited a very stable dichoptic plaid perception with clearly defined darker regions at the intersections of darker bars.

Finally, we removed the fundamental frequency from the square wave. This missing-fundamental grating did even better than the square wave in producing stable dichoptic plaid perception. All these results suggest that the high spatial frequencies contributed to stabilizing

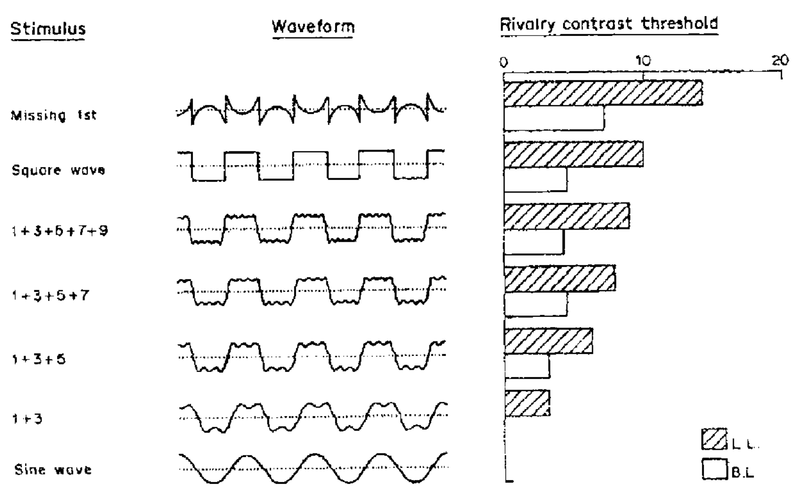

FIGURE 6. Binocular rivalry thresholds at different stages of synthesizing a square wave. The spatial frequency of the fundamental was 0.5 c/deg. Three cycles were shown in the window. The duration of the stimuli was 2 sec. The waveforms are shown on the left and the bar graph on the right shows the rivalry thresholds for each waveform. For the sine wave (fundamental alone), dichoptic plaid perception broke into binocular rivalry during the 2 sec stimulus presentation even at threshold contrast. When more harmonics were added, a stable dichoptic plaid could be seen for 2 sec and could tolerate higher contrasts.

dichoptic plaid perception and that, conversely, binocular rivalry was stimulated by the presence of the low frequency fundamental wave in the composite square wave pattern.

Experiment VI. A survey

Beside laboratory experiments, we have shown the low contrast orthogonal grating stimuli to many of our colleagues and visitors. Most of them could see a stable combination of the two eyes' images. To test the consistency of dichoptic plaid perception in a larger population, we also conducted a survey. Ten second-year optometry students were randomly chosen and shown slides containing stimuli similar to those in Fig. 1, viewed through a handhold stereoscope. All students were naive about the purpose of the survey. Sketches of possible perceptual outcomes for each pair of orthogonal gratings, a plaid, a horizontal grating, a vertical grating and a piecemeal suppression pattern were given to the observers. The observers were instructed to view a slide pair as long as they wanted and indicate which one of the sketches was similar to what they saw. The observers were also asked to describe the stability of the perception. Eight out of ten students, after viewing the dichoptic stimuli, selected the sketch of the plaid and they all reported stable percepts. The other two students had strong eye dominance. They could see only the stimulus presented to their dominant eye. This survey suggests that dichoptic plaid perception is not confined to sophisticated laboratory setups and experienced observers, but can be obtained for a large portion of the population.

DISCUSSION

The observations show that dichoptically-presented orthogonal gratings can be combined in a summative fashion when the contrast is low. Under optimal conditions, the dichoptic plaid perception can last many seconds without being interrupted by rivalry. The two eyes' views are combined uniformly across the field. The stability of dichoptic plaid perception depends on stimulus parameters such as spatial patterns, luminance, spatial frequency and contrast. These properties of dichoptic plaid perception distinguish it from the false fusion phenomenon, which has been reported not to show such stimulus dependencies (Wolfe, 1983).

Although dichoptic plaids can be seen under a wide range of conditions, they are also fragile, being crucially dependent on the relative strength of two eyes' inputs. Imbalanced physical stimuli or uncorrected refractive errors such as astigmatism can destroy the plaid perception and cause rivalry. But why is rivalry generated when the contrast is high, no matter how carefully the physical stimuli are balanced and the eyes are corrected? One possible answer would be that high contrast stimuli would initiate other processes in the visual system, such as adaptation, fatigue and saturation. The balance of these processes between the two eyes are not guaranteed. This is especially true in the presence of internal noise which is independent between the two eyes. The random fluctuation of noises may be sufficient to trigger rivalry between two patches. Another testable hypothesis would be that, with low contrast dichoptic stimuli, both the strength and the spatial extent of the suppressive effects generated by the conflicting contours may be reduced, so that neither pattern can gain dominance.

The role of spatial frequency in dichoptic plaid perception

Some of our results are consistent with the suggestion that high spatial frequencies facilitate dichoptic plaid perception (Livingstone & Hubel, 1987), but we are hesitant to reach this conclusion. In our experiments the same number of cycles of gratings were kept in the apertures as the spatial frequency varied. Perhaps a fusible aperture not only provides a target for fusion but also exerts some influence in its vicinity to reduce the strength of suppression. The longer duration of the 6 c/deg grating in Expt I and the high binocular rivalry thresholds seen in Expt IV can then be explained by the geometry of the aperture, since the region adjacent to the rim accounts for an increasing proportion of the aperture area as aperture diameter is decreased. Although the precise role of a sharp-edged aperture in stabilizing dichoptic plaid perception has not been determined, qualitative observation indicates that the more cycles are present in an aperture, the less stable is the dichoptic plaid perception (see Fig. 1). This can be explained if we assume that the scope of the fusional or suppression-reducing effect of the rim of the aperture is not limited by retinal distance but by the number of cycles of a grating pattern. The fusional effect would then be confined to a narrower band along the rim of the aperture when gratings of higher spatial frequency are used. If the fusional influence fails to cover the whole aperture, rivalry will ensue. This agrees with our observation that when the dichoptic plaid perception breaks, rivalry always starts from the center of the aperture.

Further evidence arises from Expt V, where either adding more high spatial frequency components (square-wave gratings) or taking away low spatial frequency components (missing fundamental gratings) facilitated dichoptic plaid perception. At first sight, this would appear to agree with the notion that high spatial frequency components facilitate dichoptic plaid perception. But it could well be that the spatial spread of rivalrous influence operates under the same principle as the spatial spread of fusional influence from the aperture rim. The rivalrous influence would arise from the opposition of local contours throughout the aperture and diminish when high spatial frequency components dominate the stimulus. Liu, Schor and Tyler (1989) found that the spatial spread of suppression effect was related to the spatial frequency of the rivalry targets. Using narrow band stimuli (difference of Gaussians i.e. DOG patterns) and an experimental paradigm developed by Kaufman (1963), they were able to show that the suppression zone produced by a narrow DOG was smaller than that produced by a wide DOG. In the current experiment, when more high spatial frequency components were added to the stimulus, the suppression zone shrank; the suppression effect was confined more to the vicinity of the intersections of sharp edges; a larger portion of the pattern was freed from the influence of suppression, so that the zones of a stable combination of the dichoptic stimuli extended throughout the figure. These results demonstrate that the optimal stimulus for the dichoptic plaid perception would be a few cycles of orthogonal square wave grating enclosed by a high contrast aperture.

Dichoptic plaid perception and monocular rivalry

When orthogonal sinusoidal gratings of low spatial frequency were used, dichoptic plaid perception was not very stable even near threshold contrast. The dichoptic plaid percept was sustained for 1 or 2 sec and then the two gratings would start alternating in a gradual way. Nevertheless, such alternation is not necessarily incompatible with stable dichoptic plaid perception. When the spatial frequency was 2 c/deg or lower, even a monocularly viewed physical plaid would undergo orientational rivalry and continual fading of one or the other component (Campbell & Howell, 1972; Atkinson, Campbell, Fiorentini & Maffei, 1973), similar to what we have seen under dichoptic conditions. This monocular rivalry is attributable to the reinforcement or attenuation of one grating component by its own afterimage during random eye movements (Georgeson & Phillips, 1980; Bradley & Schor, 1988). It is possible that, at low contrast, factors such as eye movements and afterimages, which contribute to monocular rivalry of low spatial frequency plaids, also contribute to the perceived alternation of dichoptic gratings under conditions of low spatial frequency and low contrast. However, the fact that binocular rivalry usually occurs in local patches suggests that interocular suppression at high contrast is mediated by local spatial mechanisms.

Implications for theories of binocular vision

The similarity of the perceived dichoptic plaid to a physical plaid challenges the two major theories in binocular vision (see Kaufman, 1974; Tyler, 1983). According to the "suppression theory", we see alternately through one eye at a time (Verhoeff, 1935). But in the dichoptic plaid perception, the two dissimilar monocular images reach consciousness at the same time and their effects are added up point by point over the space. Evidently, no suppression of either eye's target is occurring during this process. On the other hand, according to the "fusion theory", if two monocular patterns are similar then they can form a combined cyclopean image, but the two half-pictures will lose their own identities; if the two patterns are dissimilar then they are alternately inhibited by the rivalry mechanism (Panum, 1858). In dichoptic plaid perception, however, dissimilar monocular images stay together in harmony. Both contribute to a unified perception (forming higher contrast areas at the intersections of the bars) but still retain their own distinct properties (orientations, for example).

Whether the appearance of the dichoptic plaid similar to that of physical plaid is a complicated question. We noticed that there is a subtle difference between the appearance of a dichoptic plaid and a binocular plaid, that is, an identical plaid in each eye. The dichoptic plaid perception retains an impression of binocular luster (Helmholtz, 1896) while a binocular plaid looks more solid. This difference is not obvious at near threshold contrasts but becomes more and more evident as the stimulus contrast is increased. Westendorf, Blake and Yang (1991) have showed that observers could always tell the difference between dichoptic plaids and binocular plaids, although they did not specify what was the basis of this discrimination. However, Liu, Tyler and Schor (1991) have found that if dichoptic plaid was presented side by side with a monocular plaid (a physical plaid of appropriate contrast in one eye and a blank field in the other), the observers could not tell the difference between the two. We postulate that the key difference between these experiments was whether binocular luster was present in the stimulus compared with dichoptic stimulus. Westendorf *et al.* (1991) used binocular gratings which were fusible and had no binocular luster. It could well be that their observers discriminated the dichoptic stimulus by simply detecting binocular luster. On the other hand, Liu *et al.* (1991) used a physical plaid in one eye and a blank field in the other eye. The comparison stimulus, when combined binocularly, also had a lustrous appearance. At the low contrast levels tested, weak binocular luster from both monocular plaid and orthogonal gratings were very similar. Any discrimination between the two had to be based on other properties of the percept such as contrast and stability. Therefore dichoptic plaid can look very similar to physical plaid if binocular luster in the two stimuli properly equalized.

The lighter and darker blobs seen at the intersection of dark bars are created by the binocular interaction. They were simply not there in either monocular stimulus. It is certainly a possibility that the two gratings would activate two sets of orientation detectors simultaneously when there is no rivalry. These two streams of orientation signals would be kept separate until at some late stage where they were resynthesized according to certain cognitive rules. The problem with this scheme is that the stimulus involved here is a highly artificial situation which can hardly be encountered outside of a laboratory. It is hard to imagine how and why such cognitive rules or heuristics would have arisen.

It is more plausible to invoke a mechanism which can implement point-by-point spatial summation of the dichoptic stimuli but only becomes manifest when binocular rivalry does not occur. The neural substrate of this summation could well be binocular cortical cells without orientational selectivity. It has been shown that if an orientational-selective binocular cell is stimulated by orthogonal gratings, the activity of the cell is inhibited (Ohzawa & Freeman, 1986a, b) and should not signal the presence of a dichoptic plaid. Moreover, there is no known evidence in normal visual systems that monocular cells with very different preferred orientations converge to a binocular cell.

Non-orientational-selective binocular cells however, are not scarce in the visual cortex. It is often not appreciated that a large proportion of neurons in both visual areas 17 and 18 of monkey cortex have been found to be non-orientational-selective (Dow, 1974; Baizer, Robinson & Dow, 1977). Baizer, Robinson and Dow (1977), for example, found that about 50% of the cells in area 18 of awake monkeys, which were all binocular, showed weak or no orientational selectivity to stationary stimuli. Their color cells (16%), direction cells (12%), light-inhibited cells (11%) and spot cells (11%) all had round or oval receptive fields responding to stimulation of either eye. These cells, therefore, have the potential to sum up locally whatever stimuli presented to the corresponding points in the two eyes without interference from more global attributes of the stimuli, such as orientation. This substrate of non-oriented, binocular receptive fields could provide the mechanism for dichoptic plaid perception.

However, why this kind of summation is not visible in high contrast conditions (during binocular rivalry) is unclear. It is possible that, at high contrast, balanced inputs from the two eyes are either hard to attain or hard to maintain. Accordingly, the point-by-point summation mechanism could be inhibited by the dominant monocular input and has no chance to be perceived during binocular rivalry.

Our results suggest that any comprehensive theory of binocular vision should take into account not only binocular fusion, binocular rivalry and stereopsis, but also the new phenomenon of direct summation of the contour information from the two eyes.

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