

SPATIO-TEMPORAL PROPERTIES OF PANUM'S FUSIONAL AREA

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(Received 10 June 1980)

Abstract—Horizontal and vertical disparity limits of binocular fusion were examined with temporal or with spatio-temporal modulation of binocular disparity for two lines at 0.5 deg retinal eccentricity. For both horizontal and vertical disparity, Panum's fusional areas became extended by low spatial frequency variation in disparity. The horizontal extent of Panum's area also varied with temporal frequency of disparity variation. Under low spatial frequency conditions, Panum's area increased horizontally by as much as a factor of 10 (but vertically by less than a factor of 2) when temporal frequency decreased from 5.0 Hz to 0.1 Hz. At high spatial frequencies the horizontal and vertical extents of Panum's area remained almost constant (within a factor of 1.5) over the entire range of temporal frequencies. These results illustrated that Panum's area is the combination of a constant minimum area with an extended area that responds to low frequency time-varying disparities.

INTRODUCTION

Since the time of Wheatstone (1838) and Panum (1858) it has been recognized that during binocular vision similar images formed on corresponding retinal regions of the eyes appear fused into a single percept. For a stimulus at a fixed retinal locus, the retinal area upon which a target can be imaged in the other eye and appear fused defines Panum's fusional area for that particular retinal locus. Disparities that exceed this limit result in diplopia or binocular rivalry. Hence Panum's area is also a threshold measure of diplopia (Mitchell, 1966a). The classical account of Panum's area has been as a static zone of fixed extent. We are here concerned with the dynamic properties of the sensory fusional system. We first consider the role of Panum's area in relation to the dynamics of eye movements.

The presence of Panum's region is indeed fortunate for it allows the persistence of single binocular vision during stereoscopic depth perception even though there are constant changes in retinal image disparity caused by various oculomotor disturbances. For example, during binocular fixation of a stationary object, ocular drifts and saccades continually change the vergence posture of the eyes by various amounts: 15 arc sec (Riggs and Ratliff, 1951), 1 arc min (Krauskopf, 1960), 5 arc min (Hebbard, 1962) and 2–4 arc min (St. Cyr and Fender, 1969). There are also constant vergence errors known as fixation disparity that are associated with disparity-induced vergence eye movements (Ogle *et al.*, 1967). Depending upon underlying heterophoria, accommodative stimulus, AC/A ratio, and dynamic characteristics of the vergence system (Schor, 1979a), fixation disparity can be as large as 15 arc min without resulting in diplopia (Charnwood, 1950; Mitchell and Ellerbrock, 1955; Hebbard, 1962; Carter, 1964; Schor, 1979b). Inaccur-

ate oculomotor compensation for head and body movements (Steinman and Collewijn, 1980) can also result in variations of retinal image disparity during attempted binocular fixation. Panum's area provides single binocular vision in the presence of these motor-induced disparities.

While most disparities for which Panum's area compensates are dynamic, it has only been in the last decade that dynamic properties of fusion have been studied. Previously, Panum's area was considered fixed in spatial extent and independent of temporal factors. In 1967, Fender and Julesz reported that the fusional area could be extended horizontally in binocular stabilized vision by continuously increasing disparity at a rate of 2 arc min/sec. With this procedure Panum's area increased from the classical static value of 14 arc min (as reviewed by Mitchell, 1966; and Woo, 1974) to unprecedented values of 65 arc min of uncrossed disparity between two vertical lines imaged about the foveas. Since Panum's area is usually specified as the sum of the limits of crossed and uncrossed disparities which appear fused (Mitchell, 1966a), the values reported by Fender and Julesz should be doubled when compared to previously reported values. Panum's area was further extended in stabilized vision to 120 arc min uncrossed disparity using a random dot stereogram (Fender and Julesz, 1967). Recently Diner (1978) demonstrated that some of the extensions of Panum's area in stabilized vision resulted from shifts in the mean locus of the fusion range without expansion of that range. This may be interpreted as a shift in retinal correspondence for the binocular fusion mechanism. There was also evidence of an expansion of Panum's area under some conditions. Optimal velocities of changing disparity to extend Panum's area to 2 deg ranged from 2 arc min/sec to 8 arc min/sec (Diner, 1978). Velocities greater than 8 arc min/sec yielded a Panum's area similar to

classical reports. Diner (1978) estimates a decay time constant of 1 sec for a 12 arc min extension of Panum's area. A shorter decay time constant of 0.1 sec for a 120 arc min extension of fusion can be interpreted from an occlusion experiment reported by Fender and Julesz (1967). Other studies of temporal factors of fusion demonstrate a reduction in Panum's area from the classical dimension with brief pulsed disparities. Woo (1974) reports that the mean foveal size of Panum's area increased up to 4 arc min at 30 msec and remained constant thereafter. The increase in size with exposure time is explained in terms of a critical integration time in order to establish a constant size of Panum's area.

The studies of temporal aspects of binocular fusion illustrate changes in the amplitude of sensory fusion with two different classes of stimuli: fast pulsed disparities up to 30 msec where the disparity change corresponds to a minimum rate of 130 min/sec arc, and slow continuous changes in disparity (<8 arc min/sec). In the first section of this paper we have examined Panum's area with the intermediate range of dynamic disparate stimuli to determine whether temporal variations in disparity influence the amplitude of Panum's area. In a second section we consider the concurrent effects of temporal and spatial variations of disparity upon the dimensions of Panum's area.

METHODS

The basic stimulus for this study consisted of two narrow (1.5 arc min) bright lines at 0.5 deg on either side of a foveal fixation cross. In all experiments a crossed disparity in one line was presented with an equal and opposite uncrossed disparity in the other line. Methods for generating the stimuli are presented elsewhere (Tyler, 1975a). In the course of the study, we used straight lines with lengths of 90 and 15 arc min, dots with a dia. of 1.5 arc min, and counterphase sinusoidal wavy lines providing a sinusoidal disparity modulation in both time and space. The

stimuli for the first experiment are now described in more detail (see Fig. 1).

The temporal range of Panum's area was examined with horizontal disparities that were presented continuously for two sets of vertical lines (1.5 deg by 1.5 arc min) viewed haploscopically on two cathode ray oscilloscopes at a distance of 150 cm. Precautions were taken to minimize fixation disparity by adjusting the mirrors of the haploscope to neutralize the observer's heterophoria. Line thickness was minimized to heighten sensitivity to diplopia. The 0.5 deg retinal eccentricity allowed us to minimize vergence tracking with a stationary foveal fixation cross and still measure fusion ranges similar to those found at the fovea (Mitchell, 1966a; Volkman, 1859; Palmer, 1961; Ames and Ogle, 1932). Disparity between left and right sets of vertical lines was varied by displacing one set of monocular lines closer together while the contralateral eye's lines were moved apart (Fig. 1). The lines moved in counterphase so that crossed and uncrossed disparities were presented simultaneously. Thus the left line moved forward while the right line moved back in depth. This counterphase stimulus minimized possible artifacts in measures of Panum's area resulting from uncontrolled vergence tracking eye movements (Palmer, 1961; Mitchell, 1966; Fender, 1967; Woo, 1974). Tracking one stimulus to reduce its retinal motion would increase the disparity range of the other. The amplitude of displacement was increased by the method of adjustment until the disparity resulted in diplopia. Precautions were taken to minimize sensory artifacts resulting from any deviation of the horopter from a straight, frontoparallel line (Ogle, 1962; Blakemore, 1970). The sensory fusion range was centered about the fixation plane by presenting a disparity of 0.5 deg that switched at 2 Hz from crossed to uncrossed diplopia. The positions of the targets were adjusted to equalize the amplitude of crossed and uncrossed diplopia on both sides of the fixation mark. These adjustments resulted in the concurrent appearance of crossed and uncrossed diplopia during threshold measures.

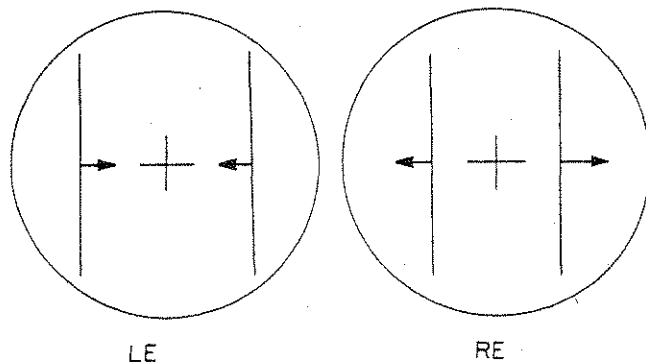


Fig. 1. Vertical lines at 0.5 deg eccentricity from a stationary fixation cross are moved laterally in opposite directions before each eye. During dichoptic viewing conditions the lines appear to move in counterphase depth.

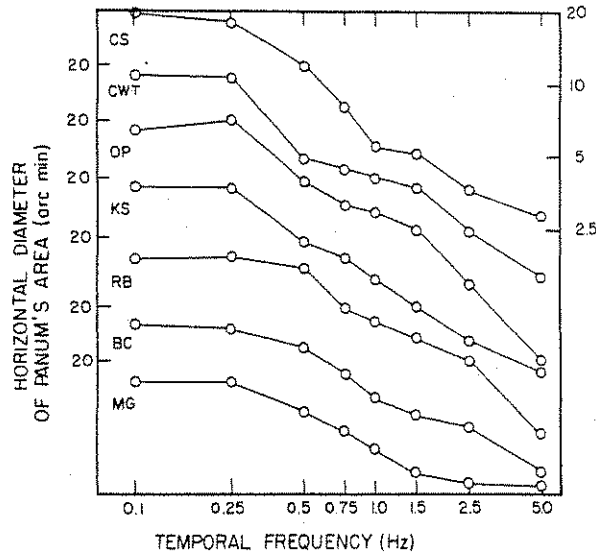


Fig. 2. The measure of Panum's area to horizontal temporal variations in disparity shown for seven observers is maximum at low temporal frequencies and is reduced to 3 arc min at high temporal frequencies. In this and the following figures the SEM was less than the size of the plotted symbols.

EXPERIMENT 1: TEMPORAL FREQUENCY RESPONSE OF PANUM'S FUSIONAL AREA

Thresholds for detecting diplopia were determined as a function of temporal frequency of sinusoidal oscillations of disparity. Temporal frequencies ranged from 0.1–5 Hz, and were presented in a randomized sequence. Observers were instructed to fixate the cross between the moving lines and to increase movement of the lines until they appeared to be doubled. The observer was instructed that if the motion in depth became left-right motion it indicated suppression of one eye. When the observer reported there was suppression, the trial was discarded. Disparity limits were computed as the mean of five settings in terms of the peak crossed to peak uncrossed amplitude of disparity for single vision at a particular temporal frequency. Seven participating observers had stereoscopic thresholds of 20 arc sec or less, normal binocular alignment, and normal corrected visual acuity. One additional observer who was a stereo-blind intermittent esotrope was studied separately.

RESULTS

Peak-to-peak disparity in arc min is plotted for all normal observers in Fig. 2 as a function of temporal frequency of the counterphase motion. Curves for individual observers have been displaced downward by a factor of 0.3 log units. References for 20 arc min are indicated along the left ordinate for each observer. The SEM for each value was less than 5% which falls within the width of the plotted symbols. Panum's area was largest at low temporal frequencies and did not change until temporal frequency was increased at

0.5 Hz. At higher frequencies Panum's area decreased to a lower limit of about 3 arc min.

The temporal frequency dependence of Panum's area was also examined for sinusoidal temporal variations of vertical disparities using the horizontal lines at an eccentricity of 0.5 deg above and below the fixation cross. In order to limit the stimuli to a more homogeneous region of the retina than 1.5 deg we reduced the length of line stimuli to 0.25 deg. The temporal frequency response of Panum's area to vertical disparities with 0.25 deg horizontal lines are compared to measures of Panum's area to horizontal disparity between vertical lines of the same length for three observers in Fig. 3. The fusion ranges for all observers were less affected by temporal frequency variations of vertical than horizontal disparity. This interesting result is taken up in more detail in the next section.

It is important to compare the values in Fig. 2 with the classical static limits for Panum's area. The literature is summarized by Mitchell (1966a), and the mean crossed to uncrossed range of horizontal disparity for all the studies he reported is 14 arc min. Mitchell (1966b) found that the range was about the same for horizontal and vertical disparities, and hence Panum's area was described as circular rather than elliptical.

We replicated the static range on our apparatus using point stimuli (1.5 arc min dia.) at 0.5 deg eccentricity based on four readings for each of two observers. The mean fusional range for horizontal disparity was 8 arc min, while the mean for vertical disparity was 9 arc min. This provides a quantitative comparison with the static values reported by Mitchell (1966b) and allows an evaluation of the dynamic results in Figs 2 and 3.

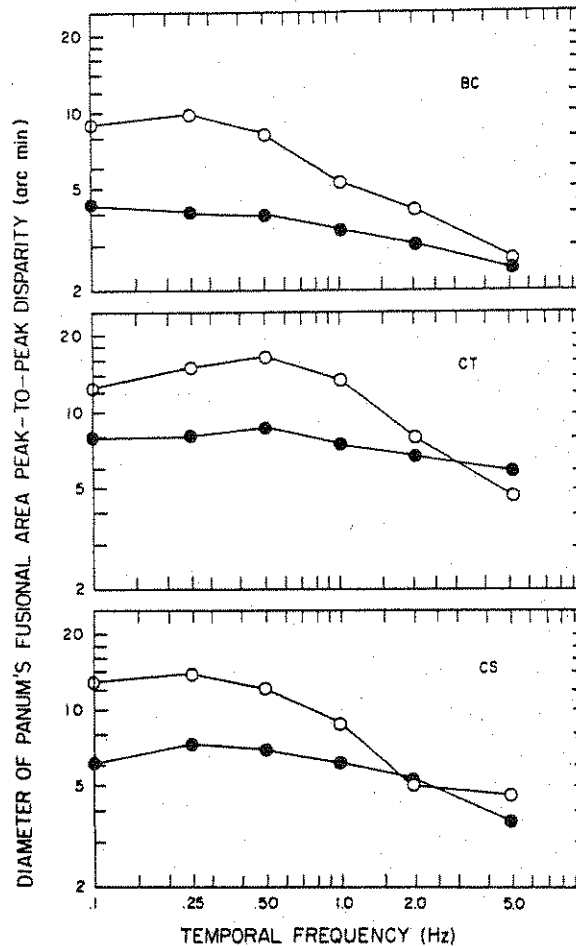


Fig. 3. Open and closed circles describe the measures of Panum's area to temporal variations of horizontal and vertical disparities respectively. The measure of Panum's area to vertical disparity is unaffected by temporal frequency for three observers.

DISCUSSION

The results of Figs 2 and 3 show that in comparison to classical dimensions, Panum's area is extended in horizontal meridian at temporal frequencies below about 1 Hz and contracted in the horizontal and slightly in the vertical meridian above 1 Hz. The low frequency range for vertical disparities is similar to the static range (~ 8 arc min), while for horizontal disparities it increased to as much as 20 arc min. Thus at low temporal frequencies Panum's area is no longer circular but becomes elliptical with an axis ratio of 2.5:1. At the highest temporal frequencies both horizontal and vertical ranges are reduced to about 5 arc min and Panum's area returns to a circular form.

We determined whether this meridional anisotropy was related to the stereo-processing mechanism by comparing the frequency response of horizontal Panum's area in a normal and stereoblind observer. This observer who had an intermittent esotropic strabismus was unable to perceive depth variation while

viewing the haploscopic stimulus described in Fig. 1. The results plotted in Fig. 4 illustrate equal temporal frequency dependence of Panum's area in both a normal and stereoblind observer for temporal frequencies greater than 0.5 Hz (although below this frequency the stereoblind observer experienced suppression; Schor, 1977, 1978). These results verify previous reports of the presence of fusion in stereoblind observers (Richards, 1971) and demonstrate that the vertical/horizontal anisotropy of Panum's area is unaffected by the absence of stereo processing.

EXPERIMENT 2: SPATIO-TEMPORAL DEPENDENCE OF PANUM'S AREA

In a previous study, Tyler (1975b) observed that the horizontal fusional area was inversely related to the spatial modulation of disparity in a vertical line as shown in Fig. 5 (top). Panum's horizontal area was larger for low than high spatial frequencies. This spatial effect is believed to account for fixation disparities

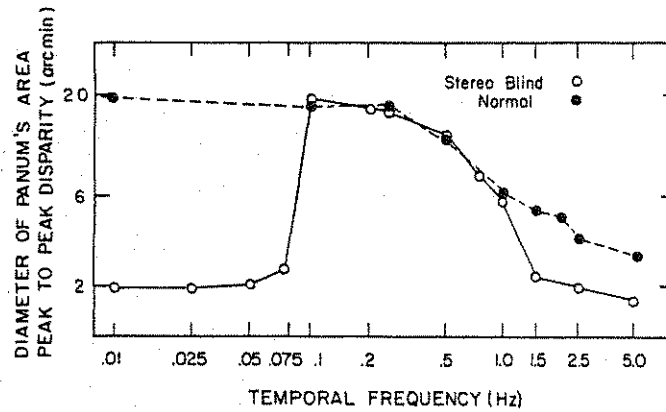


Fig. 4. The measure of Panum's area to horizontal disparities is similar for a normal and stereoblind observer at temporal frequencies greater than 0.1 Hz. Suppression disrupts binocular fusion for the stereoblind observer at lower temporal frequencies.

as large as 20 arc min measured with blurred vergence stimuli (Hebbard, 1966). We examined, for one observer, this spatial effect combined with temporal dependence of Panum's area suggested in the previous experiment by measuring the frequency response of Panum's area to temporal variations of both horizontal and vertical spatial disparities such as those illustrated in Fig. 5 (bottom).

METHOD

Sinusoidal disparities as described in Fig. 5 (top) were varied in time by modulating the amplitude of sine images seen by each eye with an AM function generator (Exact Model 519). This was accomplished by triggering the oscilloscope sweep with the input to the Y-axis which was an amplitude-modulated sine wave. The number of periods of the sine wave that appeared on the CRT was equal to the ratio of the sweep rate to the frequency of the sine input to the Y-axis. This sine input was amplitude-modulated sinusoidally at temporal frequencies ranging from 0.1–5 Hz. Thus each eye viewed a fixation cross between two vertical sine waves whose peaks and troughs oscillated horizontally in time with pendular wave motion. In binocular view, observers perceived two lines, one on each side of the fixation mark, curved sinusoidally in depth (Fig. 5, bottom). The peaks of the curved line would appear near and the troughs far away. Then they would reverse with the sinusoidal wave amplitude modulation. As shown in Fig. 5 (bottom), the left and right images about the fixation cross were varied in counterphase as were the vertical lines in Experiment 1. Line length was increased to 20 deg to allow at least two full periods of spatial frequencies as low as 0.125 c/deg.

Originally we presented straight vertical lines to one eye and sinusoidal lines to the contralateral eye as shown in Fig. 5 (top). However, we found that the

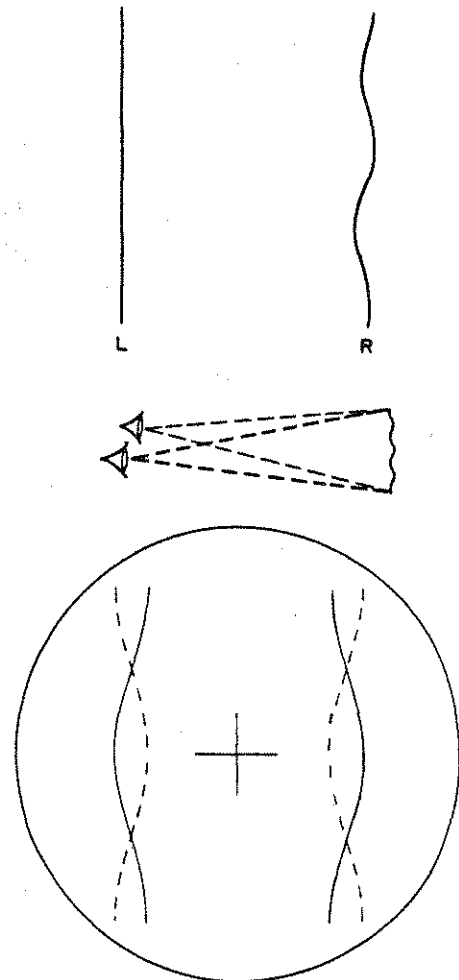


Fig. 5. The upper diagram illustrates the depth percept resulting from binocular fusion of a straight and sinusoidal line. The lower diagram illustrates one eye's target of a dichoptic pair which is perceived as two wavy lines whose sinusoidal disparities oscillate in time in counterphase. Solid and dashed lines represent two extremes the temporal counterphase stimulus.

dynamic motion of the sinusoidal line completely suppressed the visibility of the stationary straight line under dichoptic viewing conditions. Equal movements presented to both eyes eliminated the problem of monocular suppression. Even when both monocular stimuli were oscillated in time there was some suppression of the nodal points of the targets (see Grindley and Townsend, 1966 and Duensing and Miller, 1979). When suppression occurred, observers were instructed to concentrate upon the moving peaks and troughs and report when these stimuli either appeared double or moved from left to right instead of back and forth in depth. The upper horizontal disparity limits for fusion were determined as in the first experiment.

RESULTS

Figure 6 illustrates for observer CS five frequency response curves for spatial frequencies of 0.125, 0.25, 0.5, 1.0 and 2.0 c/deg modulated sinusoidally in time. As was found for static stimuli (Tyler, 1975b), Panum's area was reduced inversely with increasing spatial frequency showing disparity scaling of the fusion limit. In the temporal domain there was a high frequency roll off in these curves with a slope approaching -1 for the lowest spatial frequency. The temporal frequency slope is reduced at higher spatial frequencies, approaching zero at 2 c/deg.

We also examined the spatio-temporal dependence of Panum's area upon vertical disparities. Horizontal sinusoidal lines at 0.5 deg above and below the fixation cross were amplitude-modulated to cause temporal vertical disparity variations similar to those described above for horizontal disparities. The resulting

frequency responses of Panum's area to vertical disparities are plotted in Fig. 7 for spatial modulation of disparity ranging from 0.125 to 2 c/deg. As was found for horizontal disparities Panum's area varied inversely with the spatial frequency of vertical disparities, demonstrating disparity scaling of the fusion limit. Unlike the response to horizontal disparity, Panum's area was largely unaffected by the temporal frequency of vertical disparity. Figure 8 illustrates the orientation anisotropy of Panum's fusional region as a function of spatio-temporal variations in disparity. At low temporal frequencies the vertical range of Panum's area was 40% of the amplitude of the horizontal range. This anisotropy is depicted as an elliptical Panum's area at low spatio-temporal frequencies. Vertical and horizontal ranges were similar at high temporal frequencies as a result of the reduction of the horizontal range with increasing temporal frequency. This similarity is illustrated as a circular Panum's area at high temporal frequencies. Both horizontal and vertical dimensions decrease with increasing spatial modulation of disparity. The dependence of the vertical and horizontal dimensions of Panum's area upon spatio-temporal parameters may account for differences in previous reports of the shape of Panum's area (Mitchell, 1966b).

DISCUSSION

The large horizontal and vertical dimensions of Panum's area at low spatial frequencies suggest that cortical neurons which integrate the two monocular inputs to extend Panum's area have large receptive fields. The invariance of Panum's area at approx.

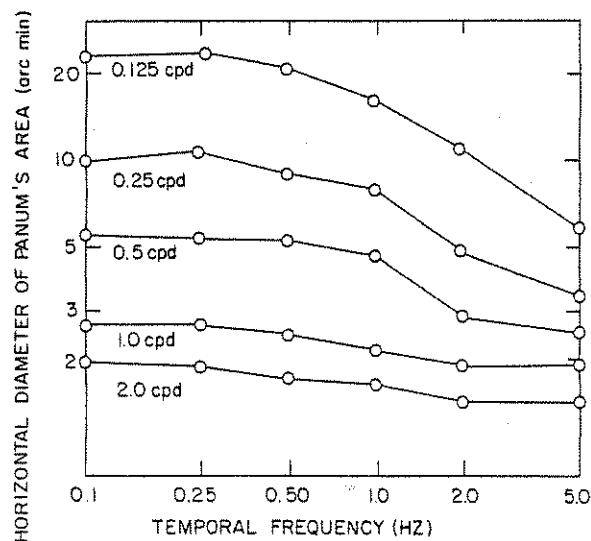


Fig. 6. The temporal frequency response of Panum's area is plotted for spatial modulation of horizontal disparities ranging from 0.125 to 2 c/deg. At low spatial frequencies Panum's area is extended to 20 arc min at low temporal frequencies and it is reduced by a factor of 10 as temporal frequency increases. At high spatial frequencies Panum's area is small and varies less than a factor of 1.5 as temporal frequency is increased. Observer C.S.

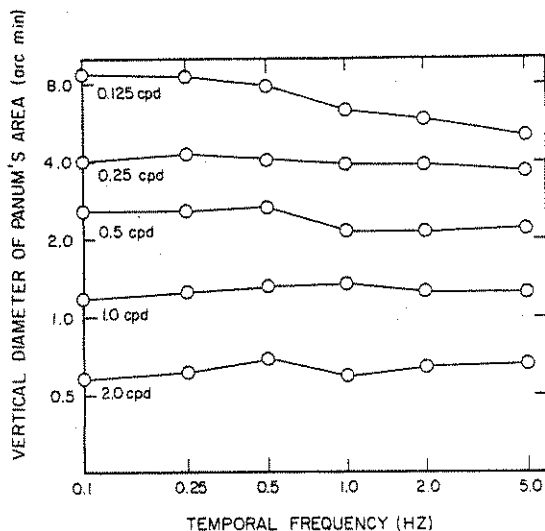


Fig. 7. The temporal frequency response of Panum's area is plotted for spatial modulation of vertical disparities ranging from 0.125 to 2 c/deg. At low spatial frequencies Panum's area varies less than a factor of 1.8 and at higher spatial frequencies Panum's area is unaffected by temporal variations of vertical disparity Observer C.S.

1.5 arc min for high spatial frequency stimuli suggests that the minimum fusion range is unaffected by temporal variations in binocular disparity. This binocular limit approaches the monocular threshold for minimum separable (Le Grand, 1953). However, our diplopia threshold to time varying disparities of high temporal frequencies are an order of magnitude greater than monocular movement thresholds (Tyler, 1975a). Indeed at high temporal frequencies the

stimuli in Fig. 5 appeared to be stationary straight lines under dichoptic viewing but when one eye was closed, the observer saw two sinusoidal lines oscillating horizontally or vertically. These observations suggest that the lower limit of Panum's area is set by binocular integration rather than monocular spatial resolution.

Thus there appear to be two separate factors that contribute to the size of Panum's area; a static limit

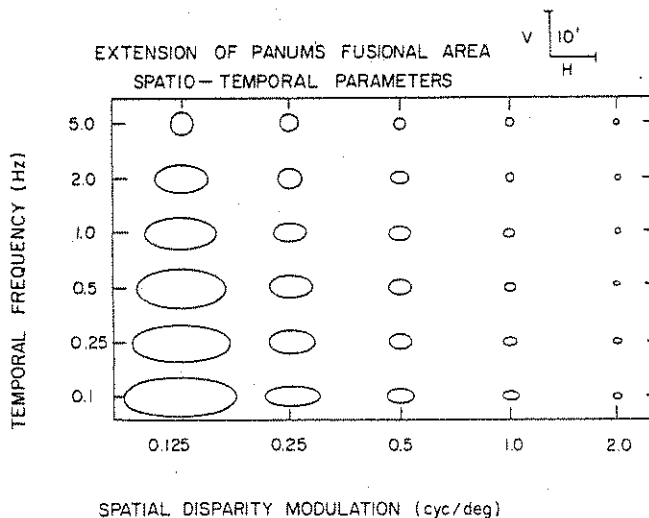


Fig. 8. The size and shape of Panum's area varies with both temporal and spatial characteristics of disparity modulation. The horizontal but not the vertical diameter of Panum's area decreases from a maximum of 20 to a minimum of 1.5 arc min as temporal frequency of disparity variation is increased. At low temporal and spatial frequencies, the shape of Panum's area is elliptical with a ratio of 2.5:1 between the horizontal and vertical extents. At high temporal frequencies the horizontal extent is reduced to equal the fixed vertical extent and the shape of Panum's area becomes circular. Both the horizontal and vertical extents are reduced to 1.5 arc min by increasing spatial modulation frequency to an upper limit of 2 c/deg. Thus both dynamic and static spatial factors determine the size and shape of Panum's area.

that varies with spatial frequency and an additional dynamic factor that depends upon temporal frequency. The static limit appears to be the only factor involved in the determination of Panum's area for vertical disparities since the vertical extent showed little variation with temporal frequency but a marked effect of spatial frequency. For horizontal disparities there is a spatial frequency dependence and an additional extension of the fusion range at low temporal frequencies. The data imply that there is both a static and dynamic component in the mechanism for horizontal fusion.

There is no indication in our data that the upper limit of Panum's area in non-stabilized vision approaches the magnitude of the horizontal sensory fusion range reported by Fender and Julesz (1967) and Diner (1978) in stabilized vision. The frequency response data presented in Fig. 6 have been replotted in Fig. 9 as a spatio-temporal surface. The surface reaches an asymptotic maximum level at low temporal frequencies. This maximum increased as we reduced spatial frequency. However, we were unable to obtain extensions much greater than 20 arc min with our lowest test spatial frequency. During

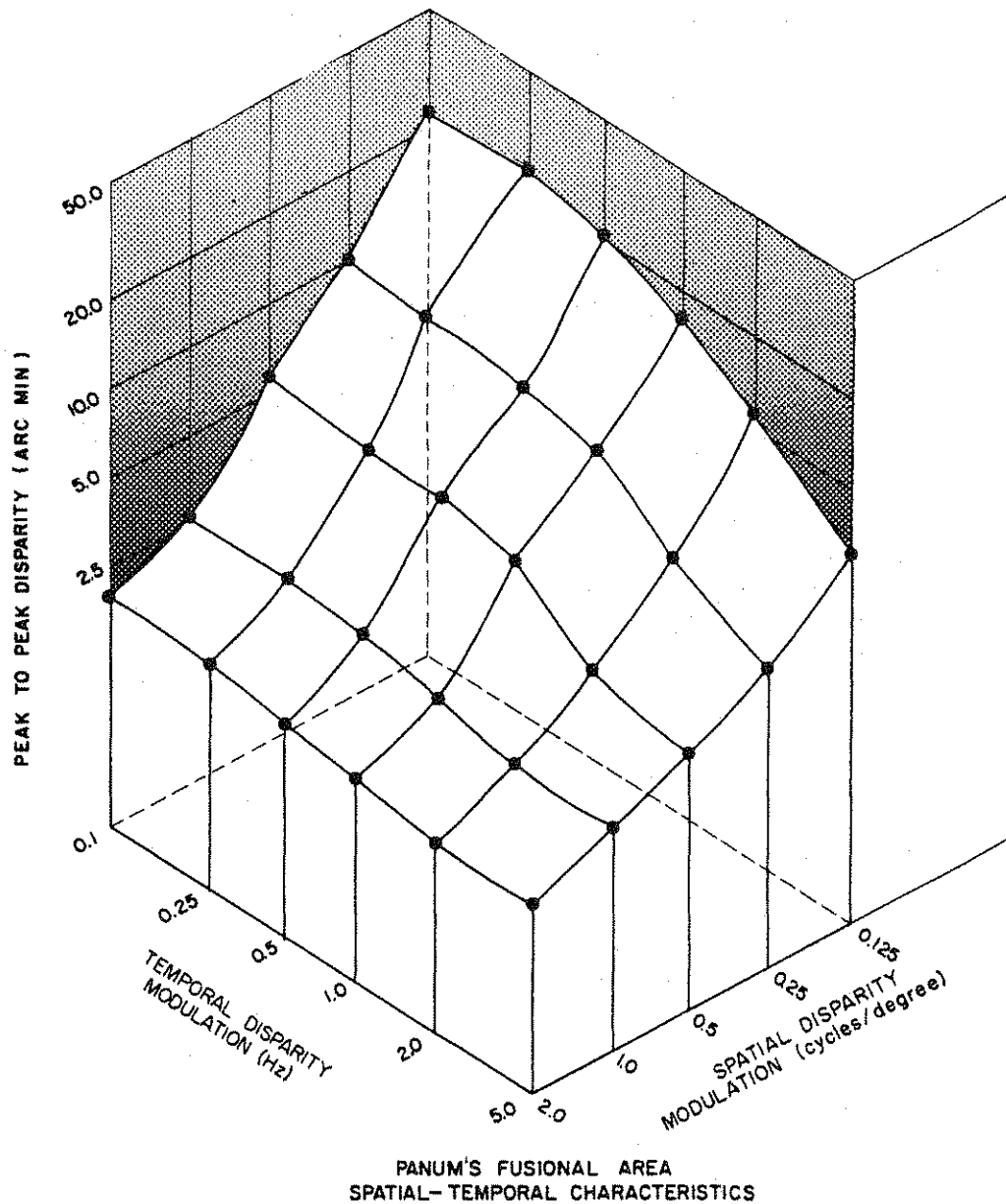


Fig. 9. Horizontal variations of Panum's area are plotted in a spatio-temporal surface, derived from the empirical data points of Fig. 6. The horizontal extension of Panum's area at low temporal frequencies at the rear of the surface results primarily from low spatial frequency variations in disparity. The minimum Panum's area shown in the forward part of the surface results from the combination of high spatial and temporal frequency stimuli.

measures of Panum's area, the stimuli involved velocities of 2 arc min/sec which are comparable to velocities that disparities increased in stabilized image studies (Fender and Julesz, 1967). How then can we account for the different amplitudes that Panum's area has been extended in stabilized and unstabilized vision? There are several possible factors. The first is that normal vergence eye movements during binocular fixation of a stationary target may have caused disparities to vary at a rate greater than 8 arc min/sec. At this rate Fender and Julesz were unable to extend Panum's area beyond classical limits in unstabilized vision (Diner, 1978). It is also possible that the large extensions of Panum's area in stabilized vision are a phenomenon separate from the variations of Panum's area reported here. We have observed that for combinations of low spatial and temporal frequency, bidirectional modulation of disparity caused symmetrical expansion of Panum's area, whereas the paradigm used by Diner (1978) involving unidirectional disparity stimuli caused an asymmetric expansion of Panum's area. Diner (1978) interprets the asymmetric expansion as a shift in retinal correspondence.

Features common to the shift in correspondence during stabilized vision and the expansion of Panum's area in nonstabilized vision include a dependence on velocity. There is also evidence that both have decay time constants. A decay time constant is indicated in stabilized vision studies by the hysteresis for refusion of diplopic targets at a smaller disparity than the extended upper threshold for diplopia. A decay time constant of an integrative mechanism is suggested for expanded Panum's area measured in the current study by the flat portion of the frequency response curve at low temporal frequencies (Figs 2-4 and 6). The corner frequency of this upper plateau of 1.0 Hz suggests a decay time constant of 1 sec. This is equal to the estimate by Diner (1978) for a 12 arc min extension of Panum's area but longer than the 0.1 sec estimated from an occlusion study by Fender and Julesz (1967) for a 120 arc min extension of Panum's area.

CONCLUSION

Panum's area should no longer be considered a fixed or constant region of single binocular vision about corresponding points. Data have been presented which clearly demonstrate the dependence of Panum's area upon spatial and temporal properties of disparity. The horizontal extent of area varies from 1.5-20 arc min. The lower end of this range is reduced in comparison with prior reports by Mitchell (1966b) by the use of high spatial frequency modulation. The upper limit is extended from classical measures of Panum's area measured with static disparities (Mitchell, 1966a). The expansion of Panum's area observed in the current investigation for horizontal but not vertical disparities appears to result from spatio-temporal integrative processes. Temporal integration may be nonlinear since comparisons of data from

stabilized and non-stabilized vision studies suggest that the decay time constant of integration decreases as Panum's area is expanded. This nonlinearity accounts for the refusion hysteresis effect observed only with large extensions. In our study a dynamic extension of Panum's area occurred for horizontal disparities beyond a static sensory fusion range. The static range is determined principally by spatial frequency factors. Thus two separate mechanisms account for the horizontal size of Panum's fusional area about corresponding points. A third mechanism revealed by stabilized image studies may extend the range of singleness by altering binocular retinal correspondence for the fusion mechanism.

Acknowledgements—This project was supported by the National Eye Institute Grant No. EY02573 and by Bio-Medical Research Support Grant No. 78-12-64 to C.S. and National Eye Institute Grant No. EY01186 and EY02124 and the Smith Kettlewell Eye Research Foundation to C.W.T.

Note added in proof—Burt P. and Julesz B. (1980) *Science* 208, 615-617, have recently verified that disparity scaling of fusion limit applies to non-periodic stimuli in the form of a fixed gradient limit.

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