Temporal integration for stereoscopic vision

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Abstract

With normal binocular vision, maximal stereoacuity requires an extended viewing duration, but the relationship between the critical viewing duration for stereopsis and other variables affecting stereoacuity is unknown. The purposes of the study were to investigate the properties of normal temporal integration for stereoscopic vision with respect to the effects of contrast and spatial frequency of the stimuli and to determine whether the temporal summation of disparity is affected in deficient stereopsis caused by abnormal binocular vision during infancy. Psychophysical methods were used to measure stereothresholds in human and monkey subjects with either normal binocular vision or abnormal binocular vision. The results showed that the critical viewing duration for stereoscopic depth discrimination was independent of variations in basic stimulus parameters and/or the subject's stereoacuity. A critical duration of approximately 100 ms was found for both local (narrowband Gabor and broadband line targets) and global (dynamic random dots) stimuli. Although stereothresholds increased with decreasing stimulus contrast, the properties of temporal integration did not. Stereothresholds were substantially elevated for monkeys and humans with abnormal binocular vision, but the critical durations for these subjects were not significantly different from those of subjects with normal binocular vision. Overall, the results demonstrate that the general properties of temporal integration for stereopsis are similar to other detection and discrimination tasks that do not require binocular processing. In addition, increased integration time does not account for the elevated stereothresholds of subjects with abnormal binocular vision.
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1. Introduction

The reciprocal relationship between stimulus duration and intensity to obtain a constant effect is one of the most fundamental properties of visual perception. Most visual tasks share this property of intensity–time, in a manner that is analogous to the integration of luminance over time as described by Bloch's law (Bartlett, 1965). Specifically, reciprocity between time and intensity occurs for viewing durations shorter than a critical duration, with constant threshold intensities for longer durations. For most visual functions, such as increment threshold (Barlow, 1958; Baumgardt & Hillmann, 1961), contrast sensitivity (Breitmeyer & Ganz, 1977; Harwerth, Smith, & Boltz, 1980; Kulikowski & Tolhurst, 1973; Legge, 1978), and monocular hyperacuities (Baron & Westheimer, 1973; Burbeck, 1986; Burbeck & Yap,

1990; Hadani, Meiri, & Guri, 1984; Watt, 1987; Waugh & Levi, 1992; Whitaker & MacVeigh, 1990), detection thresholds follow an inverse intensity–time relationship up to a critical duration on the order of 100 ms. However, stereopsis appears to be a noteworthy exception to the usual intensity–time relationships, with very reduced temporal summation and, consequently, viewing durations as long as 1000 ms may be required to achieve fine, hyperacuity levels of depth discrimination (Harwerth & Boltz, 1979; Harwerth & Rawlings, 1977; Langlands, 1929; Ogle & Weil, 1958; Shortess & Krauskopf, 1961; Westheimer, 1979, 1994). For example, in their landmark study, Ogle and Weil (1958) found only a 4-fold improvement in stereoacuity with a 125-fold increase in viewing duration for thin, line targets (local stereopsis), without a constant stereoacuity for long durations. Also in contradiction to normal temporal integration of stimulus energy for other functions, they found that stereothresholds remained at an upper limiting level (an instantaneous threshold) for durations less than 8 ms. Subsequent studies have replicated the basic finding of

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partial summation over extended viewing durations with stabilized images (Shortess & Krauskopf, 1961) and with random-dot stereograms (Harwerth & Rawlings, 1977). The more recent studies also have demonstrated complete temporal summation for the detection of relative depth with both line-contour stereograms and random-dot stereograms for viewing durations that greatly exceeded the normal integration time for luminance and/or contrast information (Tyler, 1991; Watt, 1987). Thus, the results of these studies support the idea that there are sequential stages of neural mechanisms for stereopsis (Westheimer & Pettet, 1990), and the processing time for all of the stages of stereopsis is longer than for mechanisms underlying other types of visual tasks (McKee, Levi, & Bowne, 1990).

As an alternative to the idea that binocular neurons exhibit extended temporal summation, some investigations have suggested that the lack of precise control of vergence position might account for the previous results (Uttal, Davis, & Welke, 1994). With carefully controlled convergence, reliable stereoscopic form recognition in random-dot stereograms has been demonstrated for very brief stimulus exposure times (1 ms), when the range of retinal disparity of the constituent dots was large. However, observer performance using stereograms having small ranges of disparity was less reliable, suggesting that viewing duration may be a limiting factor near stereothreshold.

Numerous factors that affect stereoacuity, such as the contrast and spatial frequency, might also affect the temporal integration properties of stereopsis. Although early studies (Lit, Finn, & Vicars, 1972; Ogle & Weil, 1958) found that, as long as the targets were clearly visible, contrast had a minimal influence on stereoacuity, more recent studies have shown effects that are predictable from the response properties of cortical neurons, which are presumed to constitute the substrate for stereopsis (Barlow, Blakemore, & Pettigrew, 1967; Crawford, Harwerth, Smith, & von Noorden, 1996; Cumming & Parker, 1999, 2000; Poggio, Gonzales, & Krause, 1988; Smith et al., 1997). Thus, stimulus variables such as contrast (Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Howarth, 1986) and spatial frequency (Harwerth, Smith, & Siderov, 1995, 1996; Schor, Edwards, & Pope, 1998; Schor & Wood, 1983; Schor, Wood, & Ogawa, 1984; Westheimer & McKee, 1980) that affect the response properties of binocular neurons also affect stereoacuity and, possibly, the temporal integration of stereoscopic disparity information.

Hypothetically, any alteration of the response properties of binocular neurons and stereoscopic depth perception could also alter the critical duration for temporal summation of binocular disparities. In this respect, the most powerful force for degrading binocular vision is early abnormal visual experience (Harwerth, Smith, Crawford, & von Noorden, 1990; von Noorden,

1985; Wiesel, 1982). Although the neurologic and behavioral effects of strabismus and amblyopia on stereopsis of human patients or animal subjects are well studied (Birch, Stager, & Everett, 1995; Cleary, Houston, McFadzean, & Dutton, 1998; Crawford et al., 1996; Harwerth, Smith, Crawford, & von Noorden, 1997; Smith et al., 1997), the extent to which the reduced binocular capabilities also affect the temporal summation of binocular disparity is not known.

The present investigations were undertaken as a broad study of temporal summation for stereoscopic vision. Separate studies were conducted on the effects of (1) the spatial frequency and contrast of stereoscopic stimuli, (2) the form of stereoscopic stimulus, i.e., narrowband Gabor stimuli vs. broadband line stimuli vs. dynamic random-dot stereograms, and (3) the stereodeficiencies caused by abnormal binocular vision during infancy. Further, to provide the broadest generalizations of the results, all of the investigations were preformed with both human and monkey observers. Some of the results of these studies have been presented briefly elsewhere (Fredenburg, Harwerth, & Smith, 2001, 2002).

2. Methods

2.1. Animal subjects

The animal subjects were rhesus monkeys (*Macaca mulatta*). Three of the monkeys were normally reared controls and twelve were experimental animals reared with a period of abnormal binocular vision during infancy. For three of the experimental subjects, normal development of binocular vision was temporarily disrupted by surgical esotropia during infancy. The exact duration of strabismus was not documented, but they had normal eye alignment when their training and testing was started at two years of age. The other experimental animals were reared with a period of alternating monocular defocus (Wensveen, Harwerth, & Smith, 2001). Alternating defocus was produced by negative-powered, continuous-wear contact lenses, which were alternated between eyes on successive days from three weeks to nine months of age. By this procedure, the infant monkeys never experienced clear simultaneous binocular vision, but the period of monocular clear vision every other day prevented the development of amblyopia. Each of the control and experimental animals had participated in other studies of binocular vision and their stereoacuities were well documented prior to the present studies (Harwerth et al., 1997; Wensveen et al., 2001). All of the animal-care procedures and experimental protocols conformed to the NIH Guide for the Care and Use of Laboratory Animals (NIH Publication no. 85-23, 1985) and were

reviewed and approved by the University of Houston's Institutional Animal Care and Use Committee.

2.2. Human subjects

The experiments were conducted on five subjects with normal binocular vision (at least 20″ stereoacuity by clinical testing) and two subjects diagnosed as microstrabismic (normal visual acuity with each eye, esotropia with interocular deviations less than nine prism diopters, and clinical stereoacuities greater than 60″) (Cleary et al., 1998; Helveston & von Noorden, 1967; Lang, 1969). These observers received extensive practice on stereoscopic depth discrimination prior to the present experiments. The experimental protocol was reviewed and approved by the University of Houston's Committee for the Protection of Human Subjects. An informed consent was obtained from each of the recruited subjects and they received remuneration for their participation.

2.3. Apparatus and visual stimuli

The main components of the experimental methods were identical for monkey and human subjects, although some of the specific details were different. The visual stimuli were generated by computer graphics (VSG2/3, Cambridge Research Systems, Cambridge, England) and presented on video monitors (model HL7955SETK, Mitsubishi, Tokyo, Japan). The monitor's pixels subtended $1.3 \times 1.3'$ at the 114 cm viewing distance used in all of the experiments. Dichoptic viewing was achieved by displaying alternate, non-interlaced frames to each eye at 60 Hz via a ferro-electric liquid-crystal shutter system (LV100P, DisplayTech, Inc., Longmont, CO) that was synchronized to the video monitor. Stimulus durations could be varied from 16.66 ms (1 frame/eye) to 1000 ms (60 frames/eye).

The visual stimuli for most of the experiments were Gabor patches, with an upper reference stimulus (3 c/deg, 50% contrast and zero binocular disparity) and a lower test stimulus (variable spatial frequency, contrast and binocular disparity). The reference stimulus had constant parameters to provide a consistent spatial localization of the reference stimulus across sessions, but differences in the spatial characteristics of the reference and test stimuli should not have affected stereothresholds when only the disparity was varied within an experimental session (Harwerth, Moeller, & Wensveen, 1998). The reference and test stimuli were vertically separated by 4 arcdeg. The Gabor patches were composed of vertical sine-wave carrier gratings that were windowed by two-dimensional Gaussian envelopes (Peli, Arend, Young, & Goldstein, 1993). The standard deviation of the vertical filter was constant (2 arcdeg), while the standard deviation for the horizontal filter varied with the spatial frequency of the carrier (two

spatial periods of the carrier grating to produce stimulus bandwidths of approximately 0.5 octave). The spatial frequency, contrast, and viewing duration of the test stimuli were unchanged for a given session, but varied across sessions. The range of binocular disparities within each session, selected to produce a systematic psychometric function, varied considerably between subjects with severe stereodeficiency and those with hyperacuity stereothresholds. In order to produce stimuli over a broad range of binocular disparities the test stimuli were drawn with combined position and phase shifts. Disparities larger than subtended by a pixel-width were generated by pixel-integer displacements of both the Gabor envelope and carrier grating. Disparity remainders or subpixel disparities were obtained by appropriate phase shifts of the carrier grating. By these means, the ranges of disparities were not limited by the spatial properties of the carrier or envelope of the Gabor patch.

To determine whether our results may differ from previous reports because of a peculiar stimulus feature, a series of experiments was conducted with stereoscopic stimuli that closely replicated the broadband stimuli used in Ogle and Weil's study of viewing durations (Ogle & Weil, 1958). The stimuli were configured as three high contrast (40%) dark lines superimposed on a bright background. The vertical line-stimuli were 4′ wide by 3.5 arcdeg high, each separated by 0.5 arcdeg. The middle line was a continuously visible fixation target and the left and right line stimuli were presented for timed periods as the reference (left line) and test (right line) stimuli. Binocular disparities for these stimuli were generated in a manner analogous to the Gabor patches. Disparities larger than subtended by a pixel-width were generated by pixel-integer displacements of the entire line, while subpixel binocular disparities were obtained by displacing a portion of the pixels of the line stimulus to create an average disparity that was smaller than the width of a pixel. The percentage of the pixel-width disparity needed to obtain a given subpixel disparity was used as the probability for displacement of pixels in the line. For the fixation and reference stimuli, the pixels were displaced in the same direction in each half-view, but for the test stimulus the pixels were displaced in opposite directions to obtain an average disparity of less than a pixel width. For example, a binocular disparity of 2″ was obtained by displacing 1/20th of the pixels in the test stimulus in each half-view. The validity of the method was assumed from an analysis of the systematic changes in depth discrimination with the signs and magnitudes of programmed disparities.

The dynamic random dot stereograms were squares of 13 arcdeg per side in overall size with a central square of 4.3 arcdeg presented with stereoscopic depth. The individual dot-elements, $6.7 \times 6.7'$ in size, were correlated between the two half-views of the stereogram, but each dot changed from dark to light with a probability

of 0.5 between successive views at 60 Hz. Stereoacuity levels of binocular disparities were obtained by disparity averaging from displacement of a portion of the dot elements in the test area (Mallot, Roll, & Arndt, 1996; Popple, Smallman, & Findlay, 1998). In some cases, this procedure may have produced occlusion cues at the edges of the disparity defined form, but they were not apparent in the dynamic display and would not have provided cues to the direction of stereoscopic depth. As with the stereoscopic line stimuli, the validity of the method was assumed from an analysis of the systematic changes in depth discrimination with the signs and magnitudes of programmed disparities. The relative dot contrast and the viewing duration were constant within a given session, but varied across sessions.

2.4. Procedures

Each trial started with the presentation of binocular fusion stimuli, which differed for each of the stimulus types. In the experiments with Gabor stimuli, the fusion stimuli were small dichoptic squares were presented at the center of the monitor screen between the upper (reference) and lower (test) stimuli. The fusion stimuli were blanked prior to the onset of the stereoscopic viewing interval. The central, continuously visible contours served as the fusion stimuli for the experiments with broadband stimuli. For experiments with random-dot stereograms, the fusion stimuli were dynamic, correlated random-dot patterns without a disparity-defined contour. The depth discrimination functions for all of the experiments were assessed via a two-alternative forced-choice paradigm for a single stimulus presentation that has been described in detail for monkey (Harwerth et al., 1995, 1997) and human (Siderov & Harwerth, 1993a,b) subjects. Briefly, each trial consisted of the following components: (1) an auditory cue to indicate the beginning of a trial, (2) a trial initiation by the subject's depression of a response switch, (3) an orienting interval of 500 ms, and (4) presentation of the stimulus for the specified duration with a coincident response interval, which was 500 ms longer than the stimulus duration. During the response interval, the subject's alternatives were: (1) a release of the response switch during the observation–response interval if the test stimulus appeared to be "nearer" than the reference stimulus or (2) a maintained depression of the response switch during the observation–response interval if the test stimulus appeared to be "farther" than the reference. A high frequency tone provided feedback for responses that were appropriately correlated with the sign of binocular disparity; i.e., for "nearer" responses given to crossed disparities and for "farther" responses given to uncrossed disparities. For monkeys, a small amount of juice reward was also provided probabilistically, for correct responses. At the end of the observation–

response interval, the video screen was blanked and a short intertrial interval commenced. Stereoscopic views of crossed or uncrossed disparities were distributed across five disparity magnitudes and presented randomly with equal probability. For monkey subjects, each session lasted two hours, or until the animal became satiated with orange juice. For human subjects each session was 400 trials.

2.5. Data analysis

For each session, the psychometric function for depth discrimination was derived from the percentage of responses of "near" as a function of stimulus magnitude, with negative values arbitrarily assigned to uncrossed disparities for purposes of data analysis. Using this convention, the normal psychometric function varied from zero "near" responses associated with the largest uncrossed disparities to 100% "near" responses for the largest crossed disparities. The depth discrimination data were fit with a logistic function (Berkson, 1953) to determine the psychophysical stereothreshold, taken as the semi-intraquartile range of the psychometric function (Harwerth et al., 1995, 1997; Simpson, 1995).

The functions for stereothresholds versus viewing durations were analyzed by an empirical model of quadratic summation, in the form of

$$\text{th} = h_0(t^{-2} + t_0^{-2})^{0.5}$$

where th is the stereothreshold at a given viewing duration (t), t_0 is the constant that determines the horizontal position of the function, which is related to the time at which the stereothreshold becomes independent of duration (critical duration). h_0 is the constant that determines the vertical position of the function and is equal to the stereothreshold when $t = t_0$. The empirical values for t_0 and h_0 were obtained by an iterative search to minimize the Chi-square statistic (Koopmans, 1981) and the asymptotic stereothreshold with extended viewing (th$_0$) was derived from the best-fit function. Thus, the data were analyzed by a model that predicts complete temporal summation for viewing durations less than the critical duration and, in log–log coordinates, the shape of the function will be constant with its lateral position determined by t_0 and its vertical position related to th$_0$.

3. Results

3.1. Local stereopsis

Thresholds for stereoscopic depth discrimination as a function of viewing time were obtained with spatially localized stimuli (local stereopsis) using both narrowband Gabor patterns and broadband extended line

Human Subjects

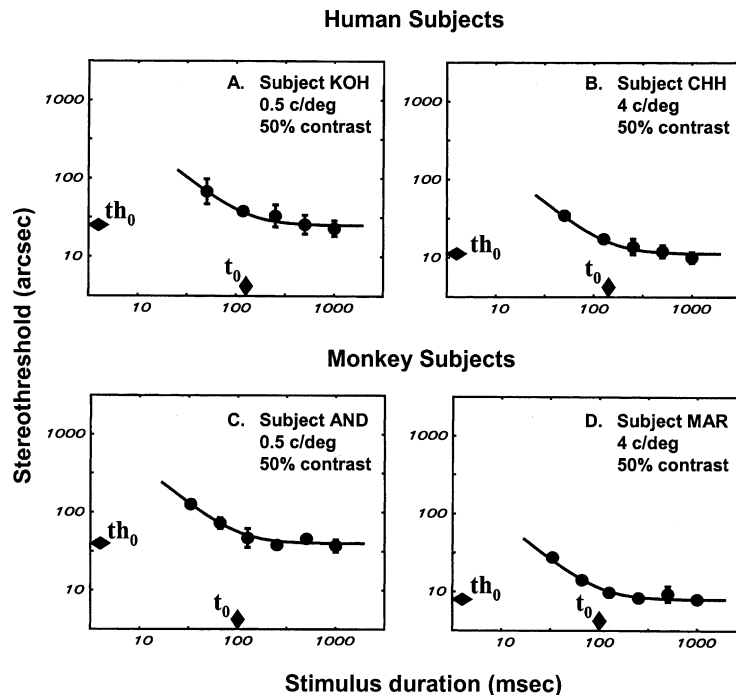## Monkey Subjects

Stimulus duration (msec)

Fig. 1. Stereothreshold as a function of viewing duration for two human (A and B) and two monkey (C and D) subjects. The stereoscopic stimuli were Gabor patterns with spatial frequency and contrast parameters designated in each graph. The solid line superimposed on each set of data represents a quadratic summation model that was fit to the data with parameters related to the asymptotic stereothreshold (th_0) and critical duration (t_0) that are indicated by the diamonds along the ordinate and abscissa, respectively. See text for other details of the data analysis.

stimuli. Typical examples of stereothreshold vs. viewing duration functions are presented in Fig. 1 for two monkeys (Subjects AND and MAR) and two humans (Subjects KOH and CHH). The stereoscopic stimuli for these data were narrowband Gabor stimuli with high contrast (50%) and either a low (0.5 c/deg; Fig. 1A and C) or a high (4 c/deg; Fig. 1B and D) spatial frequency. In all cases, the stereothresholds declined with increasing viewing duration until a constant, lowest stereothreshold was achieved, providing evidence for a critical duration for temporal summation of binocular disparity. On the other hand, the threshold-duration functions did not also show a constant threshold for very short viewing durations (i.e., an instantaneous stereothreshold).

The non-linear form of the threshold-duration data is well described by the model of quadratic summation, as shown in Fig. 1. The solid lines superimposed on the data were derived by the best fitting functions from the model, with the values derived for th_0 and t_0 that are indicated by the diamond symbols on the ordinate and abscissa, respectively. The Chi-square goodness-of-fit test ($p < 0.001$) confirmed that the model provides an excellent description of the data in each case.

Comparisons of the data for humans and monkeys indicate that the functions are indistinguishable across species. For both species, stereopsis obeyed the tenets of Bloch's law, demonstrating time-intensity reciprocity for stereothresholds when the viewing durations were brief

and constant stereothresholds with longer durations. The characteristics of the functions also exhibit the expected threshold versus spatial frequency relationships for narrowband stimuli (Harwerth et al., 1996; Schor et al., 1984); the stereothresholds (th_0) varied with spatial frequency from approximately 10″ for the 4 c/deg stimulus to 30″ with the lower spatial frequency. Remarkably, the critical period of temporal summation (t_0) was about 100 ms and was independent of stereothreshold.

Similar relationships were found for the investigations of temporal summation and stereothresholds as a function of contrast. These effects are illustrated by the examples in Fig. 2 for two monkeys with normal binocular vision and in Fig. 3 for two monkeys with abnormal binocular vision. Especially for the monkeys with normal stereopsis, a reduction in stimulus contrast caused a systematic elevation of stereothreshold without an apparent effect on the critical period for intensity–time integration. With either a low (Fig. 2A and C) or high (Fig. 2B and D) spatial frequency, the change in stereothreshold as a function of contrast was essentially proportional at all viewing durations, causing vertical shifts in the locations of the temporal summation functions, without lateral shifts. In these respects, the effects of contrast and spatial frequency were similar.

In comparison to the monkeys with normal binocular vision, the relationships between stimulus contrast and stereothreshold were not as systematic for the
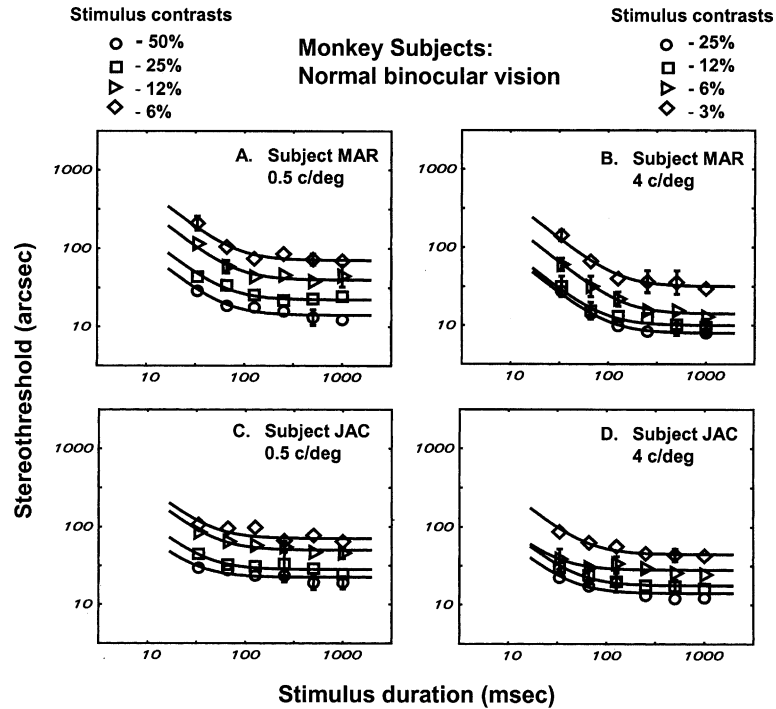
Fig. 2. Stereothreshold as a function of viewing duration for two monkeys with normal binocular vision. The stereoscopic stimuli were Gabor patterns with spatial frequency parameters designated in each graph and contrasts indicated at the upper-left for A and C and at the upper-right for B and D. The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.
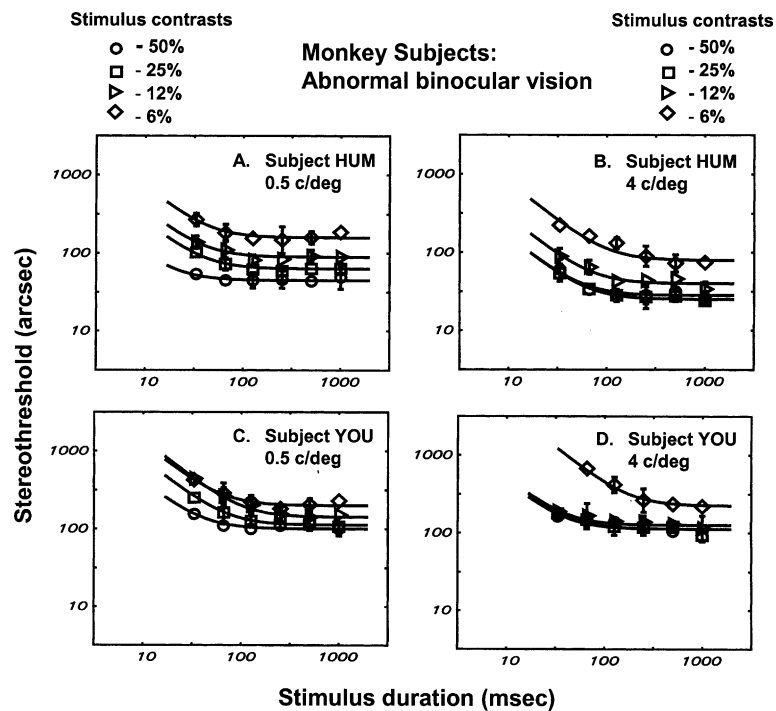

Fig. 3. Stereothreshold as a function of viewing duration for two monkeys with abnormal binocular vision caused by alternating monocular defocus during their infancy. The stereoscopic stimuli were Gabor patterns with spatial frequency parameters designated in each graph and contrasts indicated at the upper-left for A and C and at the upper-right for B and D. The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.

stereodeficient monkeys, although the critical durations for temporal summation were not altered by their reduced capacity for stereoscopic depth perception. These results are illustrated by the examples of the stereothreshold vs. viewing duration functions for two monkeys reared with alternating, unilateral defocus presented in Fig. 3. Interestingly, the elevations in stereothresholds with reduced contrasts were smaller for the stereodeficient than for the normal monkeys. In the most obvious example, the threshold vs. duration functions with a 4 c/deg stimulus (Fig. 3D) were constant for the three highest contrast levels of 50%, 25%, and 12%, with critical durations on the order of 50 ms. Thus, although the position-disparity response properties of the neural detectors may have been altered by early abnormal visual experience, the mechanisms for temporal integration of binocular disparity were not affected.

The data for monkeys with normal (Fig. 2) versus abnormal (Fig. 3) binocular vision suggests that many of the response properties of deficient stereopsis can be modeled in a subject with normal stereopsis by a reduction of stimulus contrast. The similarity of the response characteristics of normal stereopsis with low contrast stimuli and abnormal stereopsis with high contrast stimuli are demonstrated by the data in Fig. 4A. In this example, a reduction in contrast of a 0.5 c/deg Gabor stimulus from 50% to 6% caused the stereothreshold for the normal subject MAR to be increased to a position that closely superimposed the high-contrast function of subject KEA. However, the model is limited because the contrast gains of normal and abnormal binocular vision are different; specifically, the contrast reduction from 50% to 6% resulted in a 5-times elevation in stereothreshold for the normal subject compared to a 3.5-times elevation for the subject with deficient stereopsis.

The main differences between stereopsis associated with normal and abnormal binocular vision in monkeys were found also in humans. Fig. 4B presents the data for two human subjects with normal binocular vision (subjects CHH and JCT) and two subjects with primary microstrabismus (subjects KBH and ENB). The lowest stereothresholds of the microstrabismic subjects were elevated by an order of magnitude and, although the critical durations for temporal integration of stereoscopic disparities were shorter than for the control subjects, they were within the normal range of 50–150 ms.

The results for stereoscopic thresholds as a function of the duration of the stimulus from the present experiments are fundamentally different both in the degree of summation and the duration of summation found in prior investigations (Harwerth & Rawlings, 1977; Ogle & Weil, 1958; Shortess & Krauskopf, 1961). One of the possible reasons for the inconsistent results is a difference in stimulus characteristics, especially in the spatial frequency bandwidths of the stimuli. The primary previous investigations (Ogle & Weil, 1958; Shortess & Krauskopf, 1961) used broadband, extended lines as stimuli, rather than the narrowband Gabor patches used in the present study. Therefore, to determine whether the configurations of the stereoscopic stimuli were important factors in temporal integration, a series of measurements was made with narrow line stimuli that were constructed to replicate closely the stimuli used by Ogle and Weil (1958). The results of the experiments are presented in Fig. 5 for subjects with normal (Fig. 5A and B) or abnormal (Fig. 5C and D) binocular vision. The functions demonstrate that, although the stereothresholds (th_0) are lower with broadband stimuli, there are no consistent differences in the critical durations (t_0) for temporal summation. This generalization held over the
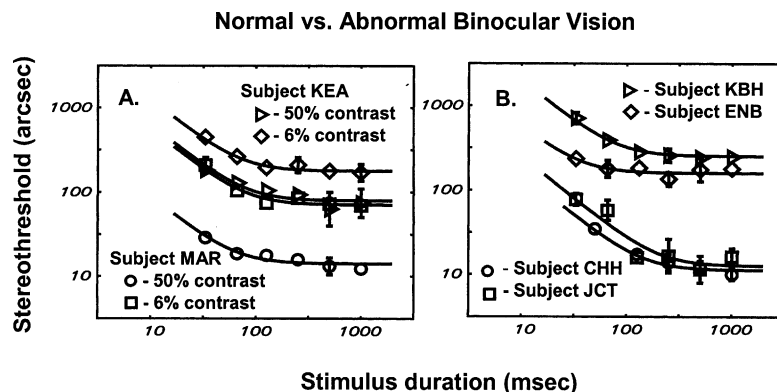
Normal vs. Abnormal Binocular Vision

Fig. 4. Stereothreshold as a function of viewing duration for monkey and human obsevers. (A) The effects of stimulus contrast on stereothresholds for a monkey with normal binocular vision (subject MAR) and a monkey with abnormal binocular vision (subject KEA). The stereoscopic stimuli were Gabor patterns with 0.5 c/deg spatial frequency and contrasts designated in the graph. (B) A comparison of the stereothreshold vs. viewing duration for subjects with normal binocular vision (subjects CHH and JCT) and subjects with microstrabismus (subjects KBH and ENB). The stereoscopic stimuli were Gabor patterns with 2 c/deg spatial frequency and 50% contrast. The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.
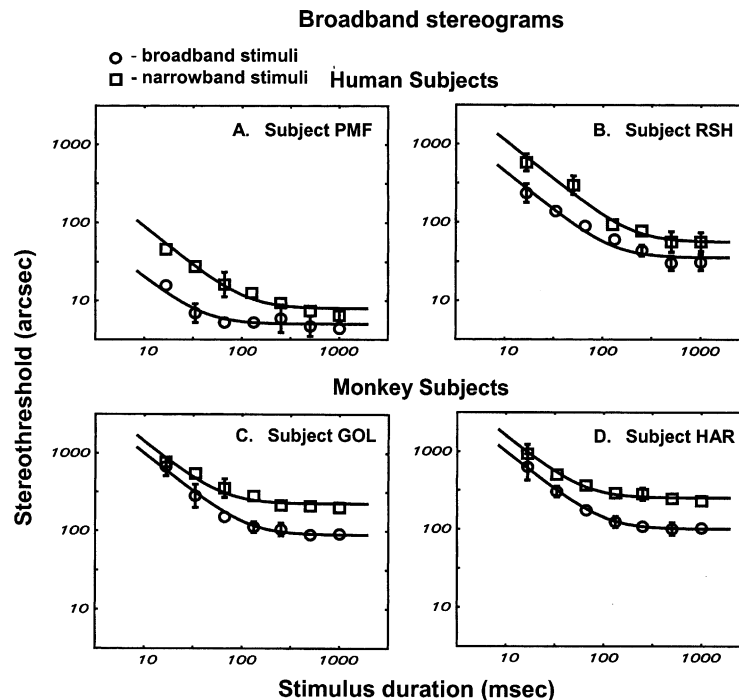
Fig. 5. The effects of the spatial frequency bandwidth of the stimulus on stereothreshold as a function of viewing duration. The stereoscopic stimuli were either Gabor patterns with 2 c/deg spatial frequency and 50% contrast (circles) or narrow-width, high contrast, line targets (squares). Data are presented for two humans with normal binocular vision (subjects PMF and RSH) and two monkeys with abnormal binocular vision (subjects GOL and HAR). The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.

range of stereothresholds that varied from very low thresholds for subject PMF, to high normal thresholds for subject RSH, to abnormal thresholds for two monkeys (subjects GOL and HAR) with abnormal binocular vision as a result of a period of surgically induced esotropia during their infancies. Thus, the extent of temporal summation for spatially localized stimuli does not appear to be influenced by the spatial arrangement of the test and reference stimuli, or by their spatial frequency content.

3.2. Global stereopsis

In addition to stereopsis with localized contours, stereoscopic depth discrimination thresholds as a function of viewing time were assessed for disparity-defined contours in random-dot stereograms (global stereopsis). The global depth observed with random-dot stereograms requires more complex processing than local stereopsis, but practiced observers can discriminate the relative depth of disparity-defined contours with very brief viewing durations (Tyler, 1991; Uttal et al., 1994). Typical examples of stereothreshold vs. viewing duration functions with dynamic random-dot stereograms are presented in Fig. 6 for four subjects: a monkey with normal binocular vision (Subject MAR; Fig. 6A), a monkey reared with unilateral defocus that caused a small elevation in stereothresholds for local stereopsis

(subject HUG; Fig. 6B), a monkey reared with unilateral defocus that caused a substantial elevation in stereothresholds for local stereopsis (subject HUM; Fig. 6C), and a human subject with normal binocular vision (subject KOH; Fig. 6D). As illustrated by these examples, the characteristics of stereothreshold vs. viewing duration functions for global stereopsis are remarkably similar to the functions for local stereopsis. Specifically, the stereothresholds (th_0) for high contrast random-dot stereograms are similar to the threshold values for Gabor-pattern stereograms composed of high spatial frequency and high contrast patterns. Further, as with Gabor-pattern stereograms, stereothresholds vary with stimulus contrast, but the critical durations for temporal integration are largely independent of the asymptotic stereothreshold.

3.3. Stereothreshold vs. critical duration

The independence of asymptotic stereothresholds and critical durations for temporal integration is further illustrated by the data in Fig. 7, which shows the relation between the two variables for all of the subjects and all of the conditions of the study (145 functions for stereothreshold versus duration measurements). In addition, Table 1 provides the parameters from linear regression of stereothreshold versus critical viewing duration for each of the four classes of stereoscopic
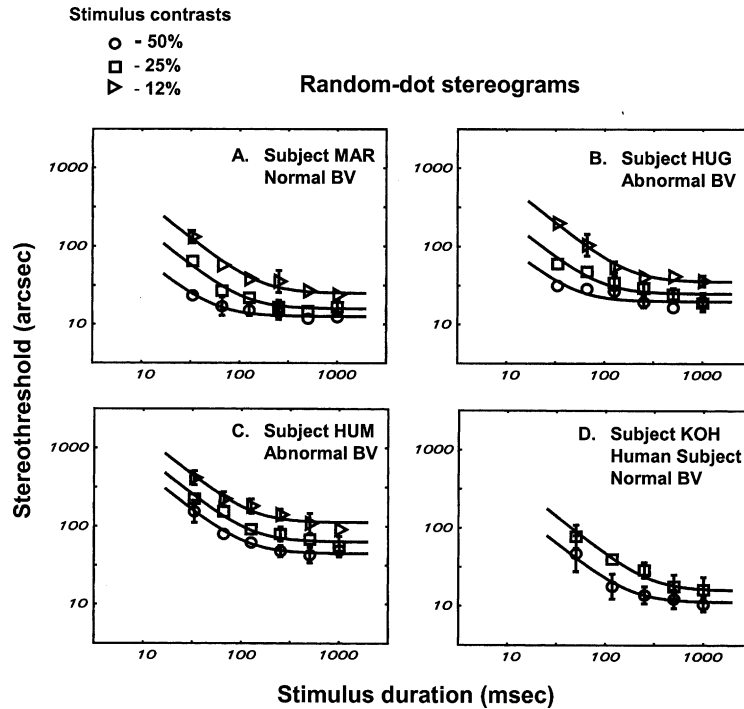
Fig. 6. Stereothreshold as a function of viewing duration with dynamic random-dot stereogram stimuli. Data are presented for four subjects, three monkeys and one human, for random-dot stereograms with contrasts indicated at the upper-left of the figure. The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.
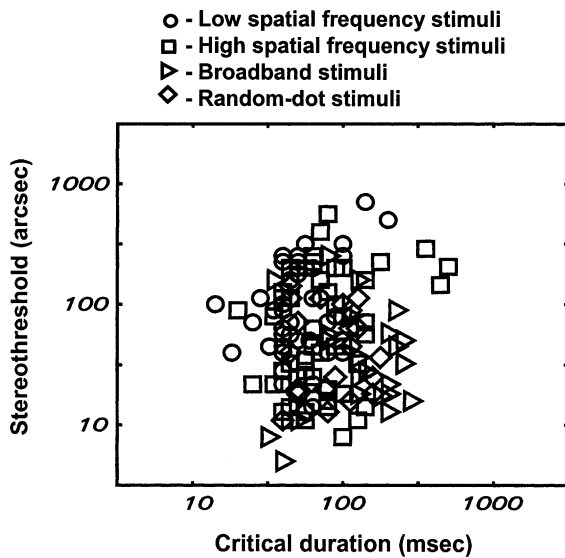

Fig. 7. Stereothreshold as a function of the critical duration for temporal summation of disparity energy. The data represent the values for the stereothreshold and critical viewing duration determined from the quadratic summation model for all of the subjects and all of the conditions of the study (145 threshold versus duration functions). The data for different stimulus types (i.e., low spatial frequency Gabor stimuli, high spatial frequency Gabor stimuli, broadband stimuli, and random-dot patterns) are represented by different symbols,

stimuli. The scatter of the data and the low correlations clearly show that there is not a systematic relationship between stereothreshold and critical duration for any of

Table 1
Linear regression parameters for stereothreshold vs. critical duration with different classes of stereoscopic stimuli (from data of Fig. 7)

	Number of functions	Slope	Y intercept	Correlation coefficient
Low spatial frequency stimuli	43	0.24	1.24	0.40
High spatial frequency stimuli	53	0.14	1.64	0.25
Broadband stimuli	23	0.06	2.00	0.09
Random-dot stimuli	25	0.05	1.83	0.09

the stimulus types (i.e., low spatial frequency Gabor stimuli, high spatial frequency Gabor stimuli, broadband stimuli, and random-dot patterns). Interestingly, although the ranges of stereothresholds and critical durations are broad, the high stereothresholds are not associated with either the shortest or longest times and, thus, abnormal efficiencies of the disparity detectors cannot explain the behavioral stereodeficiencies caused by abnormal early visual experience.

4. Discussion

The principal finding of the study was that the general characteristics of temporal summation of binocular disparity for stereoscopic depth perception are similar to

those of other visual thresholds. As with other visual functions, stereopsis demonstrates complete time-disparity summation for stereothresholds with short viewing durations and an absolute stereothreshold for viewing durations longer than a critical period of approximately 100 ms. In addition, the results show that the critical duration for temporal integration of binocular disparities is independent of the principal stimulus parameters that affect stereothresholds, such as contrast and spatial frequency, and of stereodeficiencies caused by developmental abnormalities of binocular vision, such as strabismus. These findings were consistent for measurements with localized disparate contours (local stereopsis) and with disparity-defined contours that were camouflaged in random-dot patterns (global stereopsis).

The present results differ from many previous investigations of stereopsis where the data have demonstrated a proportional improvement in stereothreshold from partial summation that extends to viewing durations of at least 1000 ms (Ogle & Weil, 1958; Shortess & Krauskopf, 1961; Watt, 1987). At first, the differences between the present and previous studies in the characteristics of temporal summation were attributed to technical differences, primarily in the types of stereoscopic stimuli that were used, and to poor control of convergence at the fixation plane in the studies with monkeys (Harwerth & Boltz, 1979). However, the results from our experiments with stimuli that closely replicated the broadband, extended lines used for the earlier quantitative measurements were the same as those for narrowband, Gabor patterns. On the other hand, the inexact control of convergence in some of the previous studies with monkeys (Harwerth & Boltz, 1979) could not be ruled out; in fact, the effect of convergence errors on stereoacuity has been exploited to study disparity vergence (Boltz & Harwerth, 1979; Boltz, Smith, Bennett, & Harwerth, 1980). Nevertheless, the technical differences do not appear to be sufficient to reconcile different conclusions about temporal summation for stereopsis and, therefore, an analysis was undertaken to determine whether the data from previous investigations were compatible with quadratic summation as a model of the integration of disparity energy. The results of this analysis are presented in Fig. 8, where data for subjects from four of the prior studies (Harwerth & Boltz, 1979; Ogle & Weil, 1958; Shortess & Krauskopf, 1961; Tyler, 1991) have been re-plotted and fit with the quadratic summation model used in the present study. The data presented in Fig. 8A and B represent data with long narrow line stimuli with either normal viewing (Fig. 8A; Ogle & Weil, 1958) or stabilized retinal images (Fig. 8B; Shortess & Krauskopf, 1961). Although this procedure does not define a unique model, the data are well fit by the summation model, and the Chi-square test of the goodness-of-fit did not reject the model ($p < 0.001$). Similarly, the data with random-dot stereograms for a human observer (Fig. 8C; Tyler, 1991) and for two monkeys (Fig. 8D; Harwerth & Boltz, 1979) also are well fit by the model. The data presented in Fig. 8D demonstrate integration of disparity energy up to about 180 ms and, thus, were expected to obey the summation model. The earlier data
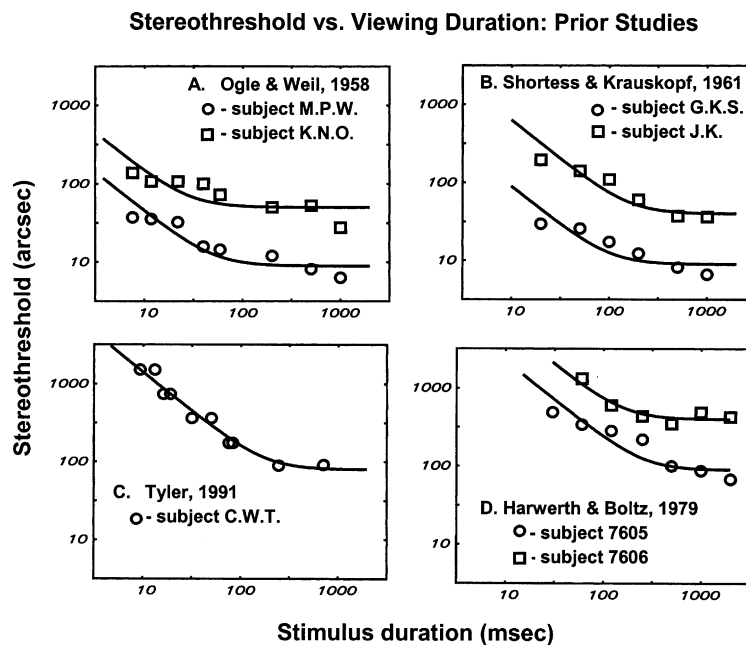

Fig. 8. Stereothreshold as a function of viewing duration for data re-plotted from four prior studies of temporal summation for stereopsis; (A) Ogle and Weil (1958), (B) Shortess and Krauskopf (1961), Tyler (1991), and Harwerth and Boltz (1979). The solid line for each set of data represents a quadratic summation model. See text for other details of the fitting procedure.

from monkeys show stereoscopic thresholds that are much higher than for humans viewing line stimuli, and also higher than for the monkeys in the present study, however, the summation model is an apt fit to the data, and the critical durations are within the normal range. Therefore, the results from both the previous and present studies suggest that the characteristics of the temporal summation of disparity energy are not fundamentally different from the temporal summation of stimulus energy for other forms of visual perception.

Many of the models of visual performance that predict more extended periods of temporal integration involve sequential processing across spatial frequency scales or across distinct classes of information, as opposed to detection by a single mechanism (Burbeck, 1986; Burbeck & Yap, 1990; Howard & Rogers, 1995; Watt, 1987; Westheimer & Pettet, 1990). In a sequential processing model for stereopsis, depth discrimination thresholds would require detection mechanisms tuned to the size and contrast of the stimulus, followed by binocular mechanisms tuned to fine disparities. Consequently, the sum of the processing times for separate serial mechanisms would be longer than for simple contrast detection. Evidence for this type of serial processing has been presented for two-dimensional acuity processes (Burbeck & Yap, 1990; Watt, 1987), as well as for three-dimensional acuities (Tyler, 1991; Watt, 1987; Westheimer & Pettet, 1990). However, because the neural mechanisms underlying monocular and binocular hyperacuity tasks are different, the quantitative effects of viewing duration are also different. For example, varying contrast to maintain equal stimulus visibilities eliminates much of the effect of viewing duration on vernier thresholds (Waugh & Levi, 1992), but not for stereopsis (Westheimer & Pettet, 1990). In a similar way, extended viewing durations produce a larger improvement for stereoacuity than for monocular width discrimination (McKee et al., 1990). The present experiments did not compare monocular to binocular performance, but showed that, while asymptotic stereothresholds are affected by non-binocular stimulus parameters, critical viewing durations are not. Thus, the results confirmed the dependence of asymptotic stereothresholds on the spatial frequency and contrast of the stimuli (Halpern & Blake, 1988; Harwerth et al., 1995, 1996; Legge & Gu, 1989; Schor et al., 1998; Schor & Wood, 1983, 1986; Schor et al., 1984; Westheimer & McKee, 1980), and also demonstrated that critical viewing durations are not altered systematically by these stimulus parameters. Therefore, the present results are explained best as reflecting the response properties for integration of the spatial frequency, contrast and binocular disparity by the first stage of binocular neurons, with subsequent stages of disparity processing relatively unaffected by stimulus duration.

Likewise, abnormal responses at the initial level of binocular vision can account for the finding that early abnormal binocular vision in either human or monkey subjects did not affect the temporal integration of binocular disparities. Rather than reflecting reduced temporal summation efficiencies, the threshold-duration functions for stereodeficient subjects were elevated over the entire range of viewing durations. The results are indicative of approximately uniform losses in the sensitivity or number of stereoscopic mechanisms, but with the residual mechanisms possessing normal tuning and disparity selectivity. Similar inferences about the neural basis of deficient stereopsis have been drawn from prior psychophysical and electrophysiological investigations of the alterations of binocular mechanisms caused by abnormal early vision (Birch et al., 1995; Crawford et al., 1996; Harwerth et al., 1990, 1997; Smith et al., 1997; von Noorden, 1985; Wiesel, 1982). Specifically, investigations of the residual binocular interactions of monkeys reared with abnormal binocular vision have shown that cortical neurons exhibit normal linear summation of contrast signals from each of the eyes, but the cells with binocular innervation have reduced binocular facilitation and lower binocular disparity tuning (Smith et al., 1997). Therefore, the psychophysical and physiological evidence support abnormalities of neurons in primary visual cortex as the neurologic basis for stereodeficiencies in strabismic or anisometropic individuals.

One other finding from the present experiments that is in exception to the classical study of Ogle and Weil (1958) is the failure to find an instantaneous stereothreshold for very short viewing durations. An instantaneous stereothreshold would be a clear violation of Bloch's law, which predicts that the intensity–time relationship should hold to the shortest time that allows detection of the stimulus. Therefore, with high contrast stimuli the stereothreshold should continue to increase with viewing duration, unless another set of mechanisms with different time constants underlies depth discrimination with very short viewing durations. As discussed earlier, the present viewing duration data are more compatible with mechanisms that integrate contrast and disparity energies and, in this respect, the data are in agreement with other studies (Shortess & Krauskopf, 1961; Tyler, 1991; Watt, 1987) that have also failed to obtain an instantaneous stereothreshold. Thus, it seems likely that instantaneous thresholds using a flash tube to illuminate the stereoscopic stimuli were responses from a transient system (Schor et al., 1998) that were not elicited by the phase-haploscope video display.

5. Conclusion

The results of the experiments have demonstrated that the basic properties of temporal integration for

stereoscopic depth discrimination are similar to other detection and discrimination tasks that do not require binocular processing. Stereothresholds as a function of viewing duration were well described by a quadratic summation model, with independent parameters related to the asymptotic stereothreshold (th_0) and the critical duration (t_0) for temporal integration of disparity energy. The critical duration was nearly constant across threshold variations caused by stimulus variables such as contrast and spatial frequency, indicating that these attributes are processed in parallel with binocular disparity. In addition, the period of temporal summation of binocular disparity was not longer for subjects with deficient stereopsis, which suggests that elevated stereothresholds of subjects with abnormal binocular vision are not caused by an inefficient integration of binocular disparities.

Acknowledgements

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