7 Binocular Fusion, Stereopsis and Stereoacuity with a Moving Head

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Constraints in Traditional Analyses of Stereopsis

Stereoscopic depth perception has been analysed in numerous laboratory experiments since Wheatstone's (1838) discovery that disparity is a sufficient and compelling stimulus for the perception of depth. One of the amazing properties of stereopsis is its extremely low disparity threshold (stereoacuity thresholds are on the order of 10″; e.g. Westheimer, 1979a). This qualifies stereoacuity as an example of hyperacuity; i.e., discriminable retinal distances are smaller than the inter-receptor distances in the fovea and the sizes of receptive fields of individual cortical neurones (Westheimer, 1979b). While such performance is remarkable enough in monocular forms of hyperacuity, such as the detection of vernier offset, stereoacuity has to cope with the additional problem that angular distances in the images on two different retinae have to be compared.

This raises the question of whether stereoacuity is in any way limited by the precision of oculomotor control, and in particular by the control of vergence. Classical studies of stereopsis have avoided this problem by minimizing eye movements, rather than dealing with it explicitly. Eye movements have been minimized in two ways.

Firstly, head movements, a major natural source of gaze instability, have been usually avoided by supporting or fixing the subject's head with chin rests or bite-boards. Needless to say, the more effective this procedure is, the less representative the experimental situation becomes with respect to the natural behavioural conditions in which stereopsis evolved.

Secondly, ocular vergence has usually been constrained to a fixation plane or a fixation point by providing each of the subject's eyes with the same visual frame of reference or fixation target. The effectiveness of such constraints on fixation has almost never been assessed by objective eye movement recordings, although subjective estimation of vergence accuracy by means of a nonius line procedure has been used in a number of studies (e.g. Regan and Beverley, 1973a,b).

Fixation points or other visual frames have effects that go beyond their control of vergence. These points and frames become part of the visual stimulus configuration where they can serve as a visual reference. Sometimes this situation is created intentionally, and the fixation mark is, in effect, one target in a stereogram, relative to which the depth of a second target is judged (e.g. Richards, 1970, 1971). In other experiments, the fixation marks are shown only intermittently, and replaced for brief periods by the complete stereogram in which depth must be discriminated (e.g. Westheimer, 1979a). Alternatively, a fixation mark has been replaced intermittently by a single target, the depth of which had to be judged relative to some fixation mark which was not seen at the same time (Jones, 1977). In many other cases, stereo-targets and fixation marks or other visual frames have been presented simultaneously while the investigators were apparently unaware of the complications created by their addition to the experimental configuration.

This is a crucial point because it means that, in the past, absolute and relative disparities have often been confused in the laboratory. The distinction between these variables is fundamental to the understanding of binocular visual processing, and this distinction is also required to understand how stereopsis can function outside of the laboratory. This point will be elaborated in the next section.
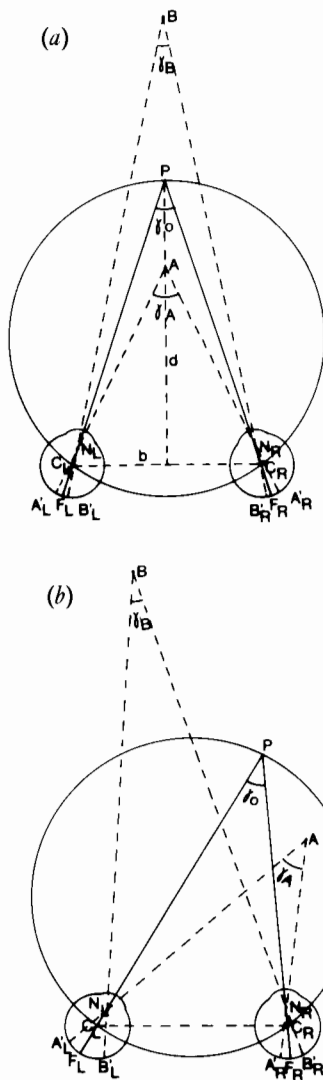
Fig. 7.1 *Angles of ocular vergence* (γ_O) *and of binocular parallax* ($\gamma_{A,B}$) *in the cases of symmetrical* (*A*) *and asymmetrical* (*B*) *convergence, with binocular fixation of target P. Solid circles: locus of equal vergence = isovergence circles. For further explanation, see text.*

Absolute and Relative Disparities

Disparity is illustrated in Fig. 7.1(a) for the simple symmetrical case, in which targets and fixation point are all located in the median plane. The eyes are converged on P, the binocular point of fixation. Ocular vergence (γ_O) is equal to the angle between the visual axes. The targets A and B have binocular parallaxes γ_A and γ_B, the angles subtended by the nodal points of the two eyes at A and B.

The absolute disparities δ_A and δ_B of A and B are:

$$\delta_A = \gamma_A - \gamma_O \text{ and } \delta_B = \gamma_B - \gamma_O \qquad (7.1)$$

Thus, the absolute disparity of a target is equal to the difference between its binocular parallax and the ocular vergence angle. For targets closer than the fixation point the disparity is positive and usually called crossed; for targets farther than the fixation point disparity is negative, and usually called uncrossed. The terms crossed and uncrossed refer to the eye-image relation when A and B are seen in diplopia: for A, the left of the two images is seen by the right eye, whereas for B, the right of the pair of two images is seen by the right eye. Crossed and uncrossed images are not to be equated with projection on temporal and nasal retinal halves, as is made clear by the more general asymmetrical case sketched in Fig. 7.1(b), in which P is displaced laterally on the iso-vergence circle through P and the centres of rotation of each eye C_L and C_R (the locus of equal vergence angles with γ_O unchanged), and A and B are located on either side of P. The parameters δ_A and δ_B are called absolute disparities, because they are scaled with respect to γ_O, which depends directly on the orientations of the lines of sight with the foveas as fixed reference points.

Crossed disparities evoke convergence; uncrossed disparities evoke divergence (Rashbass and Westheimer, 1961; for a recent review see Collewijn and Erkelens, 1989). These vergence movements tend to reduce the absolute disparity of the target. No natural targets have a target vergence smaller than zero which corresponds to optical infinity; accordingly, there is no natural need for divergence greater than that required to render the lines of sight parallel and as a point of fact most subjects can overdiverge by only a few degrees, despite the fact that their conjugate eye movements can reach temporal deviations of as much as 40–50°. The geometrical relations described thus far do not, by themselves, initiate or control vergence eye movements, any more than the retinal locations of potential targets are sufficient to initiate or control other types of eye movements, such as smooth pursuit and saccades (e.g. Kowler *et al.*, 1984). For instance, in the situation illustrated in Fig. 7.1, a decision will have to be made as to whether A or B should become the fixated target before eye movements will be made. In the real world, a multitude of targets at different distances and in different directions may be present within the visual field, all competing for visual attention. It is clear that higher-level, cognitive operations must be involved in the decision processes preceding any oculomotor action. This point was recently verified experimentally for vergence by Erkelens (1989).

It is not necessary for a target to be present at P, the intersection of the lines of sight, for the decision to fixate A or B and to induce the correct vergence response. Actually, the configuration illustrated in Fig. 7.1(b) is much

simplified because it deals only with horizontal disparities. The lines of sight may also deviate vertically in which case they would not intersect and, technically, there would be no binocular point of fixation. However, vertical disparities induce vertical vergence in a manner similar to the responses in case of horizontal disparities, at least over a limited range of vertical disparities (Houtman *et al.*, 1977; Duwaer and Van den Brink, 1981).

In the configuration sketched in Fig. 7.1, the absolute disparities of A and B, δ_A and δ_B have been defined as $\gamma_A - \gamma_O$ and $\gamma_B - \gamma_O$. These relations are valid irrespective of whether a target is actually present at P. When P is a real target, B will be seen farther away than P, and A nearer than P through the mechanism of stereopsis. A and B will be perceived as single objects (with fusion of the disparate two retinal images) as long as the absolute disparities of A and B are not too large: the range of disparities allowing fusion and stereopsis is known as Panum's area (see Tyler, chapter 2). The points A and B have a relative disparity with respect to each other:

$$\delta_{AB} = \delta_A - \delta_B = \gamma_A - \gamma_B \qquad (7.2)$$

In the latter expression, neither ocular vergence nor conjugate eye position is involved, thus relative disparity is independent of absolute retinal coordinates and independent of eye movements.

The distinction between absolute and relative disparity was clearly described by Blakemore (1969). However, the importance of this distinction has generally been overlooked. Most investigators have failed to realize that the presence of fixation points or any other visual frame of reference changes the absolute disparity of any test target only to relative disparity, of the test target relative to the fixation target. The conclusions from such studies apply only to relative disparities, but they are, nevertheless, typically treated as if they applied to absolute disparities. This confusion has grave consequences for the interpretation of many experiments because absolute and relative disparities have entirely different significance for binocular visual processing.

Stereopsis and Disparity

All classical studies that reported very low disparity thresholds stereopsis used stimulus configurations that contained relative disparities. Typically, two targets were presented simultaneously and the subject had to discriminate their depth, that is, to indicate whether one target was farther or nearer than the other target. The lowest thresholds have been found for conventional, monocularly recognizable and foveally presented, fine line stereograms. These thresholds are on the order of 10″ and less (e.g.

Howard, 1919; Ogle, 1964; Westheimer, 1979a). The observed differences in depth were, of course, relative. No judgement of absolute distance was involved.

There is only one practical way of testing the perception of depth on the basis of absolute disparities without demanding any judgements of absolute distance, and at the same time place constraints on eye position. This can only be done with successive presentation, at brief intervals, of two targets, subtending different binocular parallaxes. Under the assumption that ocular vergence does not change during each brief presentation, these successive stimuli can be chosen so as to provide known differences in absolute disparity. All other visible features, which could act as a frame of reference, should be absent from the displays. The task of the subject is to indicate whether the target presented second is nearer or farther than the target presented first.

Only a few experiments have explored such successive discriminations of absolute disparities with the potential contribution of changes of vergence minimized. Foley (1976) did very careful experiments using lines presented on an oscilloscope, with the left eye and right eye stimulation separated by crossed polarizers. A first binocular line was shown for 2 s, and after an interval of 0–32 s, a second line was shown for 100 ms at a different disparity or in a different direction. A forced-choice psychophysical technique was used with the subjects receiving feedback about their performance. No fixation point was used and, presumably, no other visual frame of reference could be seen. Discrimination thresholds increased as a function of the interstimulus time interval. They were as low as 1′ for intervals of 0–0.1 s, and rose to 20–30′ for intervals of 3.2–32 s. Thresholds for direction (successive vernier discrimination) were slightly lower than for disparity discrimination. Foley (1976) interpreted these results in the context of an earlier model of Kinchla and associates in which error accumulates over times as a result of both instability of vergence and loss of memory for the first target position.

Jones (1977) studied successive disparity detection and vergence responses to large steps in disparity (0.6–4.6°) created by the sudden replacement of a fixation point by a target with a given disparity. The second target was presented for 200 ms. These experiments were described as a follow-up of Richards' (1970, 1971) work on stereoanomalies for crossed or uncrossed disparities. There was, however, an important difference. In the experiments of Richards, a fixation point was present continuously. Thus, Richards studied discrimination of *relative* disparity, whereas Jones removed his fixation point and could, thereby, study *absolute* disparities. This difference may explain the surprisingly high proportion of stereoanomalous subjects (18 out of 30) identified in the experiments by Jones (1977). Only one third of these stereo-

anomalous subjects showed some form of anomaly in their vergence responses, and all subjects had normal stereo-acuity (better than 20″) in a standard stereoscopic test. Although Jones (1977) interpreted his large number of anomalous subjects as indicating a commonly occurring, specific defect of coarse stereopsis, the successive nature of his task seems to be a more likely explanation of the poor stereo depth-discrimination of 60% of his subjects.

The importance of the simultaneous presentation of the two targets of which the difference in depth has to be discriminated was demonstrated by Westheimer (1979a). He compared stereoacuity thresholds for ordinary, simultaneously presented line pair stereograms with those for successively presented lines at different absolute disparities. The time interval was zero, with a single binocular line executing a step in disparity and acting as a self-reference. No effective comparison stimulus was available within several degrees of visual angle. Thresholds for suc-
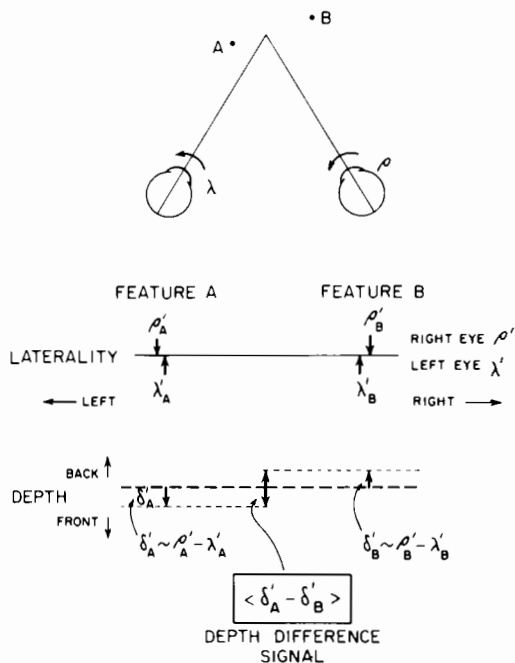
cessive discrimination were on the order of 1′, in accordance with Foley (1976); they were at least 10-fold larger than a subject's best simultaneous stereo threshold. Westheimer (1979a,b) was probably the first to express clearly that good stereoacuity requires the simultaneous presence of the targets which have to be distinguished in depth, as well as the operation of some differencing mechanism, which would extract relative disparities, independent of eye movements.

Westheimer (1979a) concluded that, though the absolute disparities δ_A and δ_B of targets A and B may be independently elaborated, a mechanism exists for the operation $\delta_A - \delta_B$, and that this differential operation makes stereoacuity insensitive to a variety of naturally occurring disturbances, including movement. His summarizing schema is reproduced in Fig. 7.2. In this schema, stereopsis derives from relative disparity, exclusively. It follows that depth, perceived on the basis of a single, absolute disparity, will be very poor or even absent.

The discussion above was restricted to stationary targets and eyes. However, the conclusion drawn has important implications for the effects of eye movements on stereopsis. These implications will be elaborated in the following sections.

Fig. 7.2 Westheimer's (1979a) *schema for a cooperative mechanism that provides high sensitivity for discrimination of depth differences and is not dependent on ocular stability. Two targets A, B are imaged on horizontal meridians of both retinas, making angles ρ_A, λ_A and ρ_B, λ_B with primary lines of sight of eyes. The images have central neural elaborations, ρ'_A, λ'_A and ρ'_B, λ'_B, and an associated representation δ'_A, δ'_B in depth domain. Sensitivity for detection of a step change in δ'_A is substantially less than for detection of difference $\delta'_A - \delta'_B$ for two simultaneously seen, optimally placed targets. This implies the existence of a differencing operation for the generation of the signal $\delta'_A - \delta'_B$ without immediate reference to the absolute values of δ'_A and δ'_B.*

Effects of Oculomotor Imperfection on Stereopsis

A first concern is whether the normal eye movements made during maintained fixation have any role in determining the limits of stereopsis. Thirty years ago they were believed to serve an essential role in dynamic theories of stereopsis, which postulated that spontaneous, miniature fixational eye movements were needed for good stereoacuity (e.g. Ogle and Weil, 1958). Shortess and Krauskopf (1961) discredited this theory by showing that stereoacuity thresholds were virtually identical under normal and stabilized image viewing conditions. In other words, stereoacuity thresholds are neither increased nor decreased by the elimination of retinal image motion.

Of particular interest, in this respect, is the instability of vergence, which can be demonstrated even during steady fixation with the head fixed. Krauskopf et al. (1960) analysed eye movements during monocular and binocular fixation using a scleral contact lens recording technique in which a beam of light is reflected from plane mirrors embedded in the surface of large, tightly-fitted contact lenses. They found that the smooth movements of the two eyes were not correlated over short periods (2 s sample intervals). Microsaccades in one eye, however, were always accompanied by simultaneous saccades in the other eye. The microsaccades in both eyes went in the same direction

and had about the same size. A few years later, Fender and Julesz (1967), also using the scleral contact lens technique, noticed the imperfect correlation of binocular eye movements in normal vision and, puzzled by the fact that this fluctuation of absolute disparity did not affect stereopsis, they proceeded to analyse this fluctuation quantitatively. They found that disjunctive drift of the order of $1's^{-1}$ slowly introduced absolute disparities. Much larger absolute disparities were introduced by imperfect yoking of the microsaccades. The probability that any saccade changed disparity by 3' or more in 40 ms was 0.57 when binocular point targets (transilluminated pinholes) were fused and the probability rose to 0.89 when a random dot pattern was fused. Some saccades produced vergence changes greater than 20'. Two years later St-Cyr and Fender (1969) confirmed the occurrence of fluctuations in vergence of at least 10' during binocular fixation (see their Fig. 7.1). Hebbard (1962), also using the scleral contact lens technique, found a maximum range of vergence of about 10' over a period of 75 s during maintained binocular fixation.

The most recent data on binocular fixation were obtained with highly precise and accurate silicone annulus scleral sensor coil techniques (see a review by Steinman *et al.* (1982). The precision of vergence (expressed as a standard deviation) during binocular fixation with the head supported on a stationary biteboard was 3' (average of five subjects) for the composite eye movement pattern, containing both smooth and saccadic eye movements.

Steady state errors, usually called fixation disparities, are known in addition to the dynamic imprecision of vergence described above. The size of these steady fixation disparities is somewhat controversial in the literature. Forced duction techniques, using prisms and nonius lines, have strongly suggested the accumulation of vergence error as a function of the amount of vergence demanded, the eye movements, invariably, being too small (Ogle, 1964; Ogle *et al.*, 1967; Crone and Hardjowijoto, 1979; Schor, 1979a,b). The errors were found to increase at a low rate as long as vergence stimuli were small, and increased more rapidly as the limits of convergence and divergence were approached. These errors have been categorized as types I, II and III (Ogle *et al.*, 1967), in which error accumulates equally fast with convergence and divergence (Type I), more rapidly with divergence (Type II), or more rapidly with convergence (Type III). The rates of vergence error accumulation differ among subjects, and also depend on the configuration of the targets. Typical disparities for a six diopters base-out prism (requiring a convergence of about 3.4°) are about 5' for type I and II subjects, but often more than 20' for type III subjects (Schor, 1979a).

Objective recordings of deficits of vergence had been reported prior to the findings just described (Westheimer and Mitchell, 1956; Tani *et al.*, 1956; Alpern, 1957). However, these early observations have been criticized on technical grounds (sometimes by the authors themselves, who seemed not to like their own results, e.g. Tani *et al.*, 1956). An influential early scleral contact lens study by Riggs and Niehl (1960) is not subject to such criticisms. Riggs and Niehl discounted the occurrence of any substantial vergence errors. They stated that vergence movements over a range of 3° were accurate to about 2'. Such values are not incompatible with Ogle's findings for fixation disparity, but of course they represent accuracy within only a very small part of the range of available vergence.

Hebbard (1962) compared subjectively measured fixation disparity with objective eye position recordings (also using the scleral contact lens technique) and found a good agreement; he measured 0.60'/prism-diopter, objectively, and 0.44'/prism-diopter, subjectively. These measurements covered a range of 20 prism-diopters base-in and base-out, corresponding to 11.3° divergence and convergence. Hebbard's findings would predict a vergence error of 3' for a convergence of 3° (1.7%). This result is compatible with Riggs and Niehl's (1960) findings and just about as good as any behaviour can be expected to be. Fixation disparity is, however, a systematic error, which increases as a function of vergence angle. Vergence errors can be expected to become rather large, in absolute terms, when convergence increases more than ten-fold to its maximum attainable angle. A more recent, direct comparison of objective (SRI double Purkinje image tracker) and subjective (nonius lines) methods, was made under more stringent conditions than Hebbard's (1962) by Kertesz and Lee (1988). They confirmed the existence of significant, systematic fixation disparities. At the same time, their study revealed considerable problems in the use of nonius lines for the estimation of the accuracy of vergence. Objective and subjective measurements usually did not agree. It was suggested that the subjective localization of the nonius lines was affected by spatial interactions, exerted by the stimulus pattern being fused.

Recent observations in our laboratory in Rotterdam (Pobuda and Erkelens, in preparation), made with the scleral silicone annulus sensor coil technique, confirm the accumulation of vergence error with increasing demands on convergence, ocular vergence being invariably smaller than target vergence. Typical errors were on the order of 20–30' at 20° convergence. Once more, these values are compatible with many of the classical findings described above.

Recently, Collewijn *et al.* (1988) described a new kind of transient vergence error that occurs in conjunction with horizontal saccades made between targets which do not require a change in vergence. In other words, binocular horizontal saccades show systematic deviations from conjugacy. The eye moving in the temporal direction has con-

sistently faster dynamics than the eye moving nasally. This results in a transient divergence. For a 30° binocular saccade, this transient vergence error has a maximum value of 1–3°, and a total duration of about 300 ms.

Most natural gaze changes between real objects in a rich visual environment involve changes in vergence as well as in version. Traditional, analytical investigations of the control of vergence do not provide this kind of stimulation. Usually, stimulation is limited, e.g., only absolute disparity can be an effective cue. Experiments of this kind produce descriptions of ocular vergence as a slow oculomotor response, with maximum velocities not much higher than about $30°s^{-1}$ (Rashbass and Westheimer, 1961; Erkelens, 1987). It is hard to understand how effective vergence could be achieved in everyday life with such poor dynamics. However, recent experiments, using a more natural stimulus configuration (real targets within a structured environment), have shown that natural smooth vergence eye movements are very much faster (up to about $150°s^{-1}$), and natural vergence is to a great extent accomplished by saccades of unequal size in each of the eyes – the smooth vergence component is secondary (Erkelens *et al.*, in preparation; see also Enright, 1984, 1986 for hints of what would be observed when vergence was measured with a high bandwidth technique).

In conclusion, on the whole, binocular control of the eye position in the artificially stabilized head is good, but far from perfect; absolute disparities of up to a degree or more are probably common during the fixation of objects, especially when they are near. Significant errors also occur during gaze changes from one to another object. Such vergence errors, whose exact size can only be measured with objective eye movement recording methods, do not seem to perturb stereopsis.

Effects of Head Movements

The discussion in the previous section on oculomotor control was limited to conditions in which efforts were made to prevent head movements, allowing eye movements to be studied, as much as possible, in a stationary frame. In ordinary behaviour the head is unsupported and is always moving (Skavenski *et al.*, 1979). These head movements are made both voluntarily and involuntarily. In ordinary behaviour, the head movements are counteracted by compensatory eye movements, which include re-fixation saccades, the vestibulo–ocular response and smooth pursuit. In the last decade, however, it has become increasingly clear that such compensation is not perfect, and as a consequence, natural gaze is not precise. This lack of precision has two components: defects in the control of gaze direction for a single eye (a problem that can be investigated in

monocular experiments) and defects in the coordination of the movements of the two eyes, causing errors of vergence in addition to errors in version (a problem that can only be investigated in binocular experiments).

There are various ways of looking at binocular coordination, depending on whether one adheres to the strict demarcation of eye movements into conjugate and disjunctive components controlled by independent subsystems – the Hering (1868) tradition, or, whether one prefers to think of a single oculomotor system controlling the movements of each eye independently in response to naturally occurring visual conditions which require the eyes to move in the same or opposite directions with respect to the median plane. There are good reasons to question the traditional view. For example, compensatory eye movements, such as the vestibulo–ocular reflex, have been traditionally viewed as strictly conjugate; this is clearly an oversimplification. Firstly, such strict conjugacy would be functionally undesirable because the geometries of the ocular and the head axes of rotation in relation to distant, but not infinite, targets, require different compensatory movements by each of the eyes. This point was elaborated by Viirre *et al.*, 1986), who showed that monkeys do actually tend to satisfy these requirements of departure from strict conjugacy. (For more general discussions of limitations inherent in traditional reflex approaches to oculomotor control see e.g. Steinman, 1986a; Collewijn and Ferman, 1988; Collewijn, 1989, 1990). Secondly, and more important in the present context, it is not reasonable to expect control of compensatory eye movements to be more precise than the control of eye movement in the stationary head (discussed in previous section). Certainly, it would be most unlikely that the binocular coordination of compensatory eye movements would reach a precision on the order of seconds or arc, the magnitude of the stereoacuity threshold. On the contrary, it seems more reasonable to expect that head movements would aggravate the imprecision of gaze demonstrated when the head is fixed in position.

The first objective evidence that head movements do indeed degrade gaze stability was obtained for the monocular situation by Skavenski *et al.* (1979), who compared gaze stability during fixation of a target at optical infinity while the subject's head was either supported on a bite-board, or unsupported with the subject sitting or standing as still as possible. Merely getting off the bite-board, without introducing any deliberate head movements, was enough to increase the instability of fixation by a factor of two to four.

Steinman and Collewijn (1980) were able to extend these observations to binocular retinal image motion during natural, active head oscillations. They found that compensatory eye movements were incomplete. There was considerable residual retinal image motion in each eye
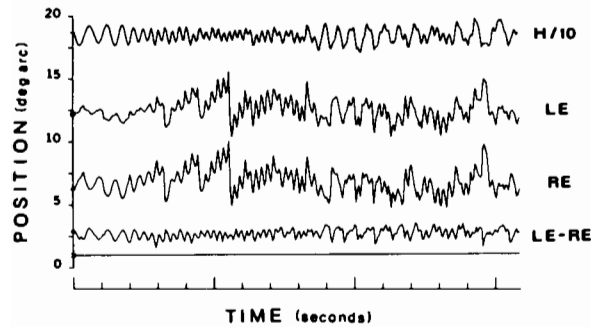
Fig. 7.3 *Recordings of head and eye movements with respect to an earth-fixed framework while the subject attempted, without success, to break fusion of a random-dot stereogram. Head swings, about 25° peak to peak, were made as rapidly as possible. Head movement has been scaled down by a factor of 10. (Steinman et al., 1985).*
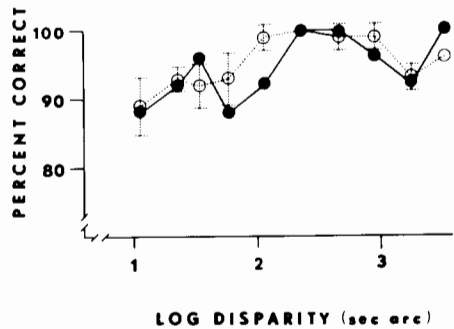

Fig. 7.5 *Stereoacuity psychometric functions during active head movements. The data points represent the average of three subjects. The closed circles show average performance when the subjects kept their heads still. The open circles show average performance when they oscillated their heads at $\frac{1}{3}$, $\frac{2}{3}$ and $\frac{4}{3}$ Hz. The error bars (s.d.) show the variability associated with moving the head at three different frequencies. (Steinman et al., 1985).*
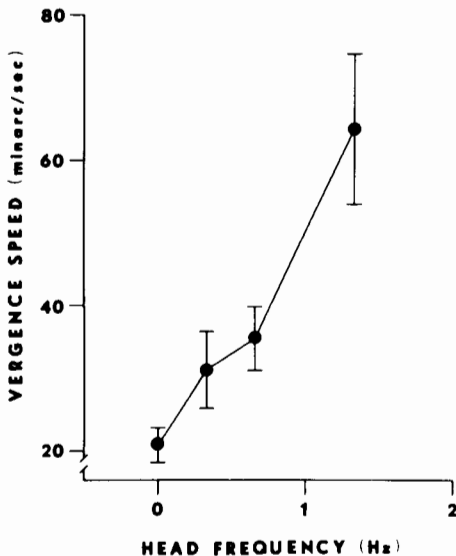

Fig. 7.4 *Mean vergence speed (absolute velocity) as a function of the frequency of voluntary head oscillation, for three subjects. The error bars (s.d.) show intersubject variability. (Steinman et al., 1985).*

angles. The most complete data on the precision of vergence can be found in Collewijn *et al.* (1981a) and Steinman *et al.* (1982). Table 1 in the latter publication shows that the standard deviation of vergence increased from about 3′ when the head was very steady while it was supported on a biteboard to about 0.5 to 1° when the head was oscillated actively or passively in the horizontal plane at frequencies between 0.33 and 1.33 Hz. The standard deviations of the positions of each of the eyes were of similar magnitude. A typical example of eye movements during voluntary head oscillation of an emmetropic, highly experienced oculomotor subject is shown in Fig. 7.3.

The velocity of vergence (difference between velocities of compensatory eye movements in each of the eyes) increased as a function of head oscillation frequency from a baseline value of about 20′ s^{-1} to more than 1° s^{-1} (Fig. 7.4).

The effects of these instabilities of gaze and vergence on stereofusion and stereoacuity were reported by Steinman *et al.* (1983, 1985). A bar seen in front of or behind a structured background served as the stereoacuity target. Stereoacuity thresholds were measured while the subject sat still and during head oscillation. Relative disparities (crossed or uncrossed, presented in a random sequence) available for these tests ranged from 11.4″ up to 58.6′. The results of the attempts to measure stereoacuity thresholds are summarized in Fig. 7.5. The available range of test stimuli was too coarse to measure a traditional threshold. Subjects correctly identified the position of the bar in the stereogram relative to the background, on more than 85% of all trials, including trials in which disparity was only 11.4″. Performance was the same regardless of whether the subject sat still or oscillated his head, and there were no reliable correlations between retinal image speed and the

(average velocities of about 4°s^{-1}). Moreover, the amount of compensation was different in each of the eyes, vergence velocities being about 3°s^{-1}. The essence of these findings has been confirmed repeatedly in subsequent experiments (Collewijn *et al.*, 1981a,b, 1983). Ferman *et al.* (1987) published the most completely controlled, three-dimensional recordings of the stability of monocular fixation of a target at optical infinity during voluntary head movements. On average, about 2.5% of horizontal and vertical head movement was not compensated by eye movements. This can lead to large errors when the head moves through large

likelihood of giving an incorrect response. These results showed that stereoacuity (with relative disparity as the only cue) is preserved in the presence of fast and large changes in vergence. In other words, absolute disparity is not an important determinant of stereoacuity threshold. Relative disparity, alone, determines the threshold.

In a second experiment, Steinman *et al.* (1985) tested the effect of head oscillations on the fusion of random–dot stereograms (Julesz, 1971). An easily-fused stereo pair was used. It showed a triangle, hovering in front of the background when it was fused (its relative disparity was 22.7′). Head oscillations (illustrated in Fig. 7.3) were made at increasing frequency in an attempt to break fusion of the stereogram. Fusion and perception of the figure-background depth-relationship was maintained, despite considerable fluctuations of vergence (i.e. absolute disparity). All efforts to break fusion were unsuccessful, even with vergence speeds reaching $8°s^{-1}$. This robustness did not depend on establishing fusion prior to the onset of head movements; all subjects tested could easily and quickly establish fusion and stereopsis of the random–dot stereogram when it was presented while the head was oscillating rapidly and while absolute disparities were large and changed rapidly.

These results were replicated in related experiments by Patterson and Fox (1984), who used dynamic random–dot stereograms showing a Landolt C in front of a background. Their stereo–display had a crossed disparity of 11′. Exposure durations of the Landolt C were varied for each of the subjects (176 to 240 ms) in order to achieve a

75% correct criterion baseline discrimination performance while the head was held still. Subsequently, their four subjects actively rotated their heads at a frequency of 0.5 or 2.0 Hz. As illustrated in Fig. 7.6 (taken from Patterson and Fox, 1984) performance was virtually unaffected by these head movements, which were comparable to those used by us (Steinman and Collewijn, 1980; Steinman *et al.*, 1982, 1983, 1985; Collewijn *et al.*, 1981a,b, 1983) and, by inference, would be likely to be associated with similar errors of vergence. (Patterson and Fox did not record their subject's movements). These findings of Patterson and Fox (1984) further corroborate the robustness of stereopsis in the presence of marked fluctuations of absolute disparity (and vergence), even when the psychophysical task was made comparatively difficult. To illustrate, (a) the random–dot stereograms were dynamic, i.e. they did not contain any monocularly identifiable features, whatsoever; (b) the task required not only a depth discrimination, but an orientation discrimination (the location of the gap) within one depth plane of the stereogram; (c) the stereograms were presented only for about 200 ms, giving subjects no opportunity to delay discrimination until some brief moment in the oscillation cycle when the vergence error happened to be small.

The reports of considerable imprecision of gaze under natural conditions by Steinman, Collewijn and coworkers were received with some scepticism by workers accustomed to believing that extremely precise binocular foveation provided the basis for effective binocular viewing (e.g. Stark, 1983). The only serious attempt known to us to refute our results experimentally was published by Duwaer (1982). He evaluated fixation stability (version and vergence) on the basis of the relative, subjectively measured, perceived distance between afterimages imprinted during fixation of a point target in the presence, or in the absence, of active head oscillation. Duwaer's (1982) results indicated a smaller dispersion of gaze than we found (standard deviations 8.7′ for direction and 3.6′ for disparity). In the absence of a direct comparison of afterimage results with objective eye position recordings, we can only speculate about whether these discrepancies are real in the sense that they arise from some unnoticed artifact of the free-head scleral silicone annulus sensor coil recordings or from artifacts in the afterimage localization technique when used to infer the position of the eyes. Ferman *et al.* (1987) discussed and examined potential artifacts experimentally and found that all known potential artifacts were far smaller than the imprecision of gaze we have recorded. This encourages us to believe that gaze is imprecise and our technique is not flawed. Alternatively, the perceived localization of successively imprinted afterimages involved central visual processing, and does not, necessarily, exactly reflect eye positions or retinal coordinates (see Steinman, 1986b, p. 1390 for a surprising exam-
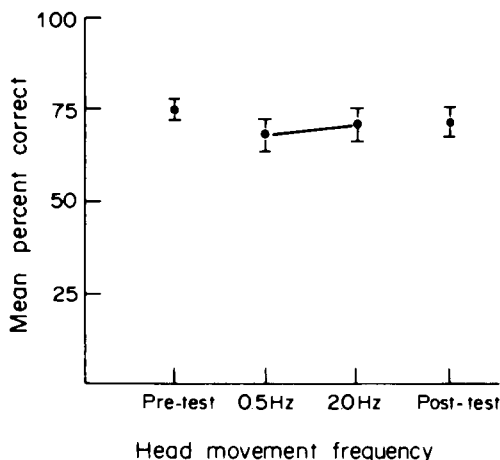

Fig. 7.6 *Mean per cent of correct recognition of the gap in a Landolt ring, forming the hidden figure in a dynamically generated random-dot stereogram. Data are shown for pre- and post-test baseline conditions, in which the head position was restricted, and for 0.5 Hz and 2.0 Hz conditions, in which the observer performed rotational head movements.* (Patterson and Fox, 1984).

ple of a discrepancy between oculomotor recording and afterimage localization techniques). An interesting, as yet unexplored, possibility is that the spatial localization of retinal images is affected by extraretinal signals (e.g. vestibular signals, or inflow or outflow signals related to oculomotor activity).

There is additional verification of the robustness of stereopsis in the presence of fluctuations of absolute disparity in situations where some unidentified measuring artifact is less likely than when eye position is measured while the head moves. Namely, the classical fixed head condition, in which the eye movements can be recorded with undisputed precision while binocular displays, rather than the head, are moved. Such experiments will be discussed in the next section. They provide unqualified support for the robustness of stereopsis in the presence of fluctuations of absolute disparity, uncontaminated by potential eye movement recording artifacts and in conditions in which such robustness cannot benefit from extraretinal information about motion of the displays on the retinae.

Effects of Various Kinds of Target Motion

Imposed, Steady Absolute Disparities

Stimulus displays, which can be moved electronically while eye positions are recorded, make it possible to perform experiments concerned with the relations among absolute and relative disparities, eye movements, and stereoscopic perception.

A pioneering experiment of great importance in this context was published by Fender and Julesz (1967). They used the scleral contact lens optical-lever technique to stabilize stereotargets, whose image separation could be varied. Two types of stereotargets were used; single line and random-dot stereograms. The line pair, once fused, continued to be fused as image separation was increased. Absolute, rather than relative, disparity was varied in these experiments because the retinal image of each display was stabilized on the retina. Absolute disparity was increased to about 60′ when fusion was broken. Once fusion was broken, image separation had to be reduced to about 40′ before the lines could be re-fused (Fig. 7.7). The result with the random-dot stereogram was similar qualitatively but very different quantitatively. Fusion was maintained as image separation was slowly increased to about 120′ before fusion was broken, and, once broken, image separation had to be reduced to about 6′ before the random-dot stereogram could be re-fused. This asymmetry was called hysteresis. The term refers to the persistence of fusion in
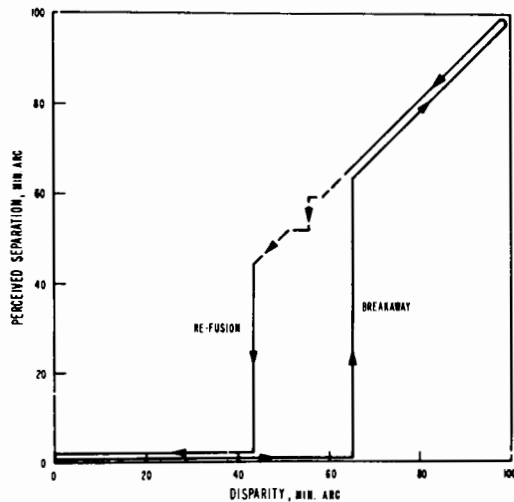

Fig. 7.7 *Breakaway and fusional limits for a single line stereotarget, moved into horizontal (absolute) disparity; stabilized vision. This diagram shows the hysteresis between loss of fusion and refusion.* (Fender and Julesz, 1967).

the presence of larger image separations than are required to reestablish fusion once fusion has been broken. In a later study, Hyson *et al.* (1983) replicated the essential findings with normal, un-stabilized vision. This was done by recording eye movements while the image separation of a random-dot target-pair was increased beyond the range of ocular divergence. Beyond this range, additional separation increases absolute disparity. They found that stereopsis and fusion were maintained for disparities up to 3° on average. They attributed this persistent fusion to a postulated process of neural remapping which occurred when such a large disparity was maintained for at least 10 s. After loss of fusion, when the maximum tolerance for disparity had been exceeded, they found a hysteresis for refusion (on average, disparity had to be reduced to 2.6°).

Hyson *et al.* (1983) also described instances (e.g. illustrated in their Fig. 5) where even after the restoration of the image separation to the initial value, and long after fusion was regained, vergence did not return to its baseline value. Vergence had changed by as much as 2° relative to the baseline measured initially. This kind of change, if real, would constitute a second and new kind of hysteresis, for which a term such as long-term neural remapping might be appropriate. However, such a phenomenon would put an end to any presently accepted or useful definition of absolute disparity or retinal correspondence. These would be continuously adapting to new values and it is unclear how vergence could still be guided reliably towards binocular foveation in the presence of such plasticity. For the moment we prefer the more conservative explanation that such apparent remappings are caused by

slippage of the contact lenses. There is evidence to support this interpretation. Erkelens and Collewijn (1985c), repeated the experiments of Hyson *et al.* (1983) with scleral silicone annulus sensor coils, and found that vergence always came back very close to its initial value when the half-images of a random-dot stereogram were first separated and then returned. They were unable to confirm the existence of long-term remapping (Fig. 7.8) with a technique known to be free from slippage artifacts. They did, however, confirm the extended Panum's area of 1 to 2°, originally reported by Fender and Julesz (1967).

More recently, Diner and Fender (1987) published results showing that the extended range of fusion for a (stabilized) single line exists in the nasal, as well as in the temporal, direction. However, the fusional range was smaller (on the order of 20') than in the original experiments by Fender and Julesz (1967). As the authors suggest, this may have been due to, what they apparently considered to be trivial, difference in the experimental apparatus. In Diner and Fender's (1987) experiments, the target was seen in the centre of a (non-stabilized) aperture with a diameter of 3°. This was probably used to maintain fixation by counteracting the strong impulse to converge the eyes when the fusional range was tested with crossed disparities. The presence of a fixed aperture is not trivial. It is an essential departure from the conditions in the original experiments because it introduced a frame of reference which changed absolute into relative disparities. The original experiment (Fender and Julesz, 1967) was
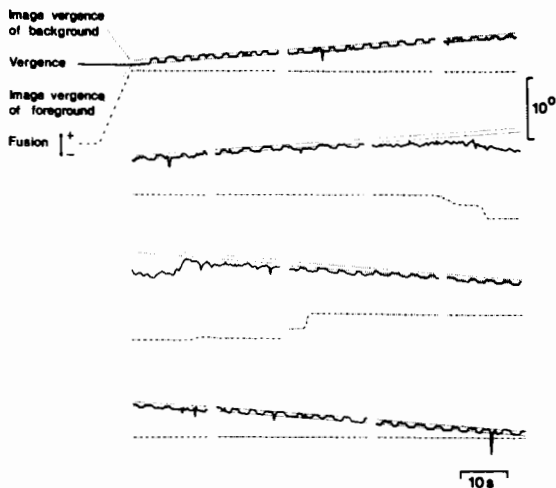

Fig. 7.8 *Recordings of ocular vergence (solid line) and target vergences of figure (lower dotted line) and background (upper dotted line) of a random-dot stereogram of which the half-images were first pulled slowly apart beyond the limit of ocular divergence, and then slowly returned to their initial position. Fusion is signalled by the stripe-dot line, halfway positions indicating borderline fusion.* (Erkelens and Collewijn, 1985c).

correctly titled *Extension of Panum's fusional area in binocularly stabilized vision.* It is important to realize that Panum's area reflects absolute and not relative disparities. This means that the Diner and Fender (1987) experiment is not relevant to the problem studied originally and it is not surprising, therefore, that they obtained confusing results.

The distinction between absolute and relative disparity and its application to studies of Panum's area has a long, and often confused history. This issue will be elaborated in the next section. In the traditional description, non-corresponding points on the two retinae, when stimulated separately, lead to different perceived visual directions (see Chapter 1, by Ono). For small disparities, simultaneous stimulation of such points by the disparate images of an object leads to perception of a single object in a particular visual direction in the fused binocular scene. This state can be called single vision. If fusion does not occur, we speak of diplopia. The maximum disparity for fused vision, beyond which diplopia occurs, is conventionally represented by considering that a point on one retina corresponds not to a single point on the other retina, but, rather, to a Panum's area of finite size (Panum, 1858; Ogle, 1964; Mitchell, 1966a,b). When defined in this way, Panum's area relates to absolute, overall disparities of the two retinal images; one of its main virtues is to allow some range of tolerance for imperfect binocular alignment. In short, Panum's area allows single vision despite instabilities and constant errors of vergence (fixation disparity). In practice, however, Panum's area is usually described as the range of disparity that allows single vision around a small fixation target. This fixation target falls near the foveal centre which means that most actual measurements of Panum's area are really estimates of the maximal relative disparity between a fixation target and some test object that allows single vision. (See Tyler, chapter 2 for an extensive treatment of measurements of Panum's area defined in this way).

The great merit of the original experiments of Fender and Julesz (1967) was, that they measured the tolerance for absolute disparity. In fact, their measurements were probably the first, ever, to measure Panum's area properly. In short, their results reflect the true Panum's area and not an extended Panum's area as they believed. Traditional determinations of Panum's area were too small because they were made in the presence of relative disparities which masked the tolerance of absolute disparities.

Note that the size of Panum's area, as determined by Fender and Julesz (1967), is consistent with the area of robustness of stereofusion in the presence of the imprecisions of vergence observed when the head oscillates (see previous section). There are, however, two puzzling differences between the Fender and Julesz and free-head experiments. Namely, the slow rate of image separation

found to be required to maintain fusion and the considerable hysteresis between the loss and reestablishment of fusion in the Fender and Julesz experiment seem not to agree with the conditions under which fusion could be maintained and established when absolute disparity was changed by oscillating the head. These puzzling differences, if they represented real differences in binocular processing, would limit the significance of Fender and Julesz's extension of Panum's area to a laboratory curiosity of little value in the coping with the dynamic instabilities of vergence demonstrated in the natural vision of moving subjects.

Fortunately, there is recent evidence that the actual dynamic properties of Panum's area are considerably better than was apparent from the experiments of Fender, Julesz and their colleagues. Piantanida (1986) replicated the experiment of Fender and Julesz (1967), confirming that fusion of random-dot stereograms was maintained up to more than 2° of absolute disparity. At the same time, he found considerably less hysteresis. Fusion was reestablished at about two thirds of the disparity at which it had been lost. Piantanida's results were still well outside the traditionally determined size of Panum's area, and similar to the hysteresis reported originally for a single line stereotarget by Fender and Julesz (1967). Piantanida attributed the difference between hysteresis in his and the prior experiment to the absence of any competing targets, i.e. he did not use the fiducial marks employed by Fender and Julesz (1967). In other words, competition between absolute and relative disparity was reduced.

Erkelens (1988) reinvestigated hysteresis and found that its magnitude could be related to the recent history of fusion in the experiment. Only absolute disparity was stabilized to prevent the image-fading, usually associated with complete stabilization. Absolute disparity was slowly increased at a rate of $6' s^{-1}$, comparable to the speeds of $2-10' s^{-1}$ in the experiments of Fender and colleagues. Both crossed and uncrossed disparities were varied. On average, fusion was maintained up to 142' and fusion was reestablished at an absolute disparity of 88' when absolute disparity was reduced after fusion had been broken. This outcome was similar to Piantanida's (1986). However, when stereograms were abruptly presented at one or another fixed absolute disparity, without an immediately prior history of fusion or rivalry, the total range of fusion was 156'! This proves that fusion is possible at very large absolute disparities without prior fusion in a smaller Panum's area, and without any slow stretching of the fusional range. This result agrees well with the perceptual observations of Steinman et al. (1985), who found no difficulty in fusing a stereogram, presented during violent head oscillations (see earlier section on oculomotor imperfection and stereopsis). Erkelens (1988) went on to study effects of prior fusional history on measurements of Pa-

num's area. He showed that unfused viewing of the stereogram for a period of 1 min, with absolute disparity set to 4°, reduced the fusional range in the same (crossed or uncrossed), but not in the opposite, direction of disparity. Unfused pre-exposure in the direction opposite to the subsequent test, reduced the total fusional range by an average of 6'. Unfused pre-exposure in the same direction as subsequently tested, reduced the fusional range by an average of 48'. This reduction could account almost completely for the hysteresis effect (142' versus 88') observed when absolute disparity is slowly increased, kept for some time beyond the limits of fusion, and then slowly reduced so as to fall, once again, within the range of fusion (see Tables 1 and 2 in Erkelens, 1988). Finally, Erkelens (1988) found that the zone of fusion extended somewhat further for crossed than for uncrossed disparities.

These results show that it is unlikely that hysteresis would occur when absolute disparity fluctuates during natural head movements unless the fusional range is exceeded for an extended time in a constant direction. This is a very unlikely state of affairs in an individual with a normal oculomotor system. It could occur in clinical cases of precarious fusion that might be caused by strong phorias.

In summary, it seems likely that Panum's area is relatively wide, i.e. there is an operational zone of several degrees, within which differencing processes are capable of establishing fusion and extracting relative from absolute disparities, as suggested in Westheimer's (1979a) schema (Fig. 7.2). Panum's area is functionally symmetrical in the sense that fusion can be established, as well as maintained, easily within this area. Once this is appreciated, neural remapping need not be invoked in naturally occurring viewing conditions and hysteresis becomes a description of a reproducible phenomenon confined to particular laboratory conditions in which the fusional history of the subject is manipulated in particular ways.

The results discussed above relate primarily to static disparities with very low rates of change (maximum $10' s^{-1}$). In the next sections, we shall examine the effects of higher retinal image velocities.

Stereopsis of Moving Targets

The effect of retinal image motion on stereoacuity was investigated by Westheimer and McKee (1978). In a prior paper, they had shown that Landolt C and vernier acuity were not adversely affected by retinal image speeds up to about 2 or $3° s^{-1}$ (Westheimer and McKee, 1975). In their experiments on stereoacuity, the target was a line stereogram, consisting of two vertical lines one above the other that was presented for 190 ms during each trial. There were four additional dots in the display outlining a square around the line stereogram. These dots were seen contin-

uously by both eyes. This square was used to define the plane of fixation and thereby establish and maintain convergence. The line targets could be moved together with respect to the fixation square. The relative disparity between the upper and lower line was varied between trials in order to measure the stereoacuity threshold. In one experiment, the upper and lower lines moved sideways. Target velocities up to $2°\,s^{-1}$ had essentially no effect on the stereoacuity threshold, which remained at about $10''$. The result was similar when only the upper line moved and relative disparity was kept constant with respect to the lower line. In this condition any monocular cue that might have influenced the measured threshold was abolished. In view of the brief exposure time, tracking eye movements were likely to be less than 10% of target speed (Kowler and McKee, 1987), so retinal image speed was probably rather similar to target speed. The results described so far show that stereoacuity is not sensitive to sideways motion. In a second experiment, Westheimer and McKee (1978) oscillated the line stereogram in depth by moving its right and left eye half-images in opposite directions, relative to the square used to maintain fixation. In this case, stereoacuity thresholds were considerably elevated with target speeds of $2°\,s^{-1}$. This result shows that motion-in-depth was more detrimental to stereoacuity than sideways motion (see also Regan and Beverley, 1973a, Fig. 2). They explained this result noting that at higher velocities of motion-in-depth, the targets were seen with 'disparity with respect to the fixation plane' for longer periods of time. Apparently, the authors were alluding, here, to absolute disparity despite the fact that relative, as well as absolute disparity, was changing in their display. They proceeded with stereoacuity threshold measurements in which the target line pair was stationary but was presented at different absolute disparities. Once again, the fixation plane was maintained by the continuously visible square of dots. Thresholds for the relative disparity between the two lines were found to rise rapidly when their absolute disparities placed them more than $2–3'$ away from the fixation plane. It is important to realize that Westheimer and McKee's (1978) experiments do not necessarily show that stereoacuity is very sensitive to absolute disparity because relative disparity also varied in this experiment. This was true because the fixation targets were continuously visible, which meant that the subject actually viewed an array of targets with two ranges of relative disparity: $3–10'$ between the fixation square and the line targets, and less than $1'$ (the threshold) between the two lines. Thus, Westheimer and McKee's (1978) results can be interpreted as showing that the presence of a large relative disparity increases the threshold for the discrimination of a small relative disparity seen at the same time.

A similar point applies to the experiments by Blakemore (1970) and Regan and Beverley (1973a), who investigated the threshold for relative disparity as a function of absolute disparity, which was varied over a larger range. Since all measurements were done with the eyes fixating a continuously present target, Blakemore's (1970) findings actually also show an increased threshold for the discrimination of one relative disparity in the presence of another (larger) disparity.

An effect of this kind was explicitly demonstrated in subsequent experiments by Westheimer (1979a), who found that a standing disparity, as small as $1'$, more than doubled the stereoacuity threshold. Similarly, Schumer and Julesz (1984) found a systematic increase in stereo-thresholds as a function of the height of depth pedestals.

In conclusion, there is evidence that sideways motion does not have adverse effects on stereoacuity. One must bear in mind, however, that the experiments supporting this conclusion were done in the presence of a fixation frame and the effects of changes in absolute disparity on stereoacuity can not be evaluated because absolute disparity was not manipulated as an independent parameter. Visible fixation frames introduce relative disparities which confound the interpretation of the results. The next section examines newer evidence which shows that, at least for extended targets of low spatial frequency, stereopsis is insensitive to fluctuations in absolute disparity even when absolute disparity varies by several degrees.

Stereopsis and Dynamic Changes in Absolute Disparity

Subjects have some ability to discriminate successively presented, absolute disparities, although it is clearly inferior to their ability to discriminate simultaneously presented, relative disparities (Westheimer, 1979a). Changes of absolute disparity are effective in the control of vergence eye movements and may, therefore, be available for perception, providing, of course, that the visual system has access to the information used to control eye position. For instance, it might not be surprising to find that subjects can discriminate between crossed and uncrossed disparities, because these different stimulus configurations lead to opposite motor responses. But, even if they can make this discrimination, we are then left with the question of whether such differences in disparity are perceived as differences in depth. If this were the case, then a continuous change in absolute disparity should induce a vivid perception of motion-in-depth.

Erkelens and Collewijn (1985a,b) have shown that this is not the case. Changes of absolute disparity, alone, do not induce perceptions of motion-in-depth. Their subjects viewed a Julesz-type random-dot stereogram (size $30 \times 30°$), which, when fused, caused a central diamond figure to be seen in front of the background. The depth difference between this figure and its background was pro-

duced by a relative disparity of 36'. The continuous perception of this stereo figure-ground configuration ensured that binocular fusion and global stereopsis were operative throughout the experiment which examined the effects of motion of each half-image of the stereogram on the perception of the stereogram as a whole. The two half-images were moved in counterphase, with a triangular waveform, whose frequency varied from 0.125–0.5 Hz and whose amplitude varied from 0.3–3°. The ratio between the amplitudes of the motion of the right and left eye half-images could also be varied. No fixation point or other frame of reference was available. The most striking observation was made when both half-images moved in counterphase at equal amplitudes. In this condition, the stereogram was continuously perceived as stationary, completely fused, and in normal depth. No motion in depth of the stereogram as a whole or of any part of it was perceived, even though careful observation revealed modest changes in apparent size (smaller size being associated with crossed disparity). Movements of the half-images at unequal velocities induced perceptions of motion. However, this motion was always sideways, never motion-in-depth. Manual tracking of the perceived motion was used to demonstrate, quantitatively, that the binocularly-perceived sideways motion was equal to the algebraic mean of the two separately, monocularly-perceived sideways motions. For equal, but opposite velocities this mean is, of course, zero and when this stimulus condition was viewed, the percept was stationary. Also, more complex stimulus combinations (e.g. half-images moving 90° out of phase) induced apparent motion, reflecting the moment-to-moment mean of the two velocities. It had been previously shown (Ono *et al.*, 1977; Sheedy and Fry, 1979) that during static convergence, the oculocentric direction of a fused image is the mean of the oculocentric directions of the two monocular images (see chapter 1). Clearly, this is also the case when the entire images on the left and right retinae are moving: binocularly-perceived motion in this condition is the mean of the two monocularly-perceived motions.

All of these observations related to absolute motion. The binocular perception of relative motion (sideways or motion-in-depth), in the presence of a frame of reference follows different rules (Regan and Beverley, 1973a,b). What was surprising about the Erkelens and Collewijn (1985a) result was that no perception of motion-in-depth was produced despite the changes in absolute disparity. The stimuli used by Erkelens and Collewijn (1985a) induced vergence movements but the eyes did not track the moving targets with perfect accuracy (Erkelens and Collewijn, 1985b) which meant that substantial changes in disparity were taking place at the retinal level. Neither these changes nor the vergence eye movements elicited the perception of motion-in-depth.

This result may seem in conflict with the many prior demonstrations in which changes in disparity were sufficient to induce perception of motion-in-depth (e.g. Wheatstone, 1852; Tyler, 1971; Richards, 1972; Beverley and Regan, 1973, 1975; Regan and Beverley, 1973a,b, 1979). However, in all of this prior research, motion was presented relative to a background or fixation point. In the experimental conditions of Erkelens and Collewijn (1985a) no frame of reference or fixation point was provided. A vivid perception of motion-in-depth was immediately induced in all subjects when a stationary reference was added to the binocular stimulus displays. When the stationary reference was small (e.g. a single bar), it was seen in motion against the stereogram which was seen as stationary. A more extended stationary reference (e.g. a grating) was seen as stationary while the stereogram, itself, appeared to move. In short, the stimulus configuration is important in the perception of induced motion-in-depth. A similar point was made for sideways motion by Duncker (1929) who suggested that a selective principle operated in induced movement conditions, namely, surrounded objects tend to be seen as moving. Similar kinds of principles probably influence induced motion-in-depth.

In the experiments of Erkelens and Collewijn (1985b) the half-images were moved sinusoidally in counterphase at frequencies between 0.25–1.5 Hz and amplitudes of 0.5–2.5°, centred around an angle of 10° convergence. It was possible to correlate the motion perceived by the subject with changes in vergence, as well as with absolute disparity because the positions of both eyes and half-images were continuously recorded. Fusion and stereopsis were maintained as long as the various frequency-amplitude combinations did not raise the velocity of the
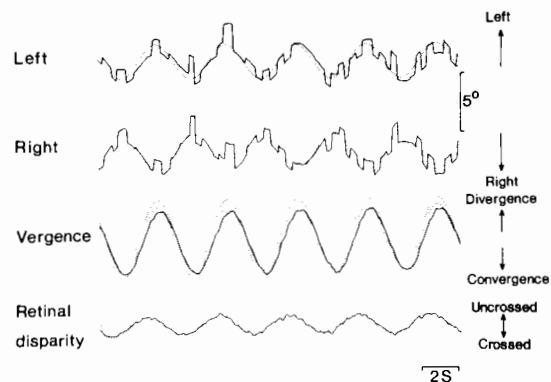

Fig. 7.9 *Relations between eye movements and oscillations of half-images of random-dot stereogram. Upper two traces: position of left and right eye (solid lines) and half-image seen by that eye (dotted lines). Third trace: ocular vergence (solid line) and target vergence (dotted lines) of background (upper curve) and figure (lower curve). Bottom trace: absolute retinal disparity changes caused by vergence tracking error. (Collewijn et al., 1986).*
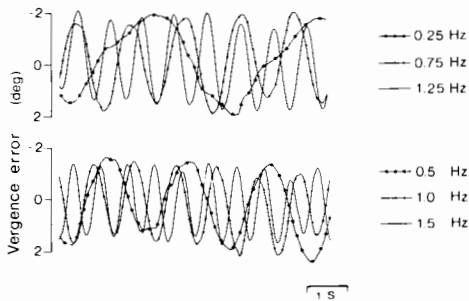
Fig. 7.10 *Examples of courses of absolute disparity at the upper limit for fusion of a large random-dot stereogram. Data from one representative subject, for different frequencies of modulation of target vergence.* (Erkelens and Collewijn, 1985b).

change in the angle between the half-images above some maximum, which varied among the subjects from 6–13.5° s^{-1}. Observations made below this limit will be discussed next. As mentioned already above (Erkelens and Collewijn, 1985a) counterphase motion of the half-images at equal amplitude did not induce perceived motion. Subjects perceived a constant figure-ground relationship in the stereogram and the entire fused display was perceived as stationary. Typical relationships between stereo half-images and binocular eye movements are shown in Fig. 7.9. Ocular vergence movements tended to track changes in target vergence because no fixation targets were provided. Ocular vergence tracking was not perfect, however. It was always smaller than changes of target vergence. This mismatch caused large, sinusoidal fluctuations in absolute disparity. As shown in Fig. 7.10, the maximal fluctuations of absolute disparity compatible with maintained fusion were independent of the frequency of oscillation and amounted to an area between 1–2° of crossed and uncrossed disparity (the width of this area varied among the subjects). This result is strikingly similar to the extent of Panum's area found for random-dot stereograms by Fender and Julesz (1967) in their experiments with stabilized viewing. Within the fusional zone, fluctuations of absolute disparity did not disturb stereopsis, nor did they elicit the slightest perception of motion in depth. The associated changes in vergence also did not elicit perceptions of motion-in-depth. However, these same stimuli, when combined with any stationary visual reference, induced very compelling perception of motion-in-depth (Erkelens and Collewijn, 1985a,b). These perceptions of motion-in-depth apparently require changes of relative disparity. Changes of absolute disparity do not elicit perceptions of motion-in-depth. This is clearly very different from the perception of sideways motion, which can be elicited by changes of absolute direction of the stimulus and/or associated versional eye movements (Erkelens and Collewijn, 1985a,b).

The observations of Erkelens and Collewijn (1985a,b)

were confirmed and extended by Regan *et al.* (1986). One important aspect of this later investigation was the comparison of the effects of variations of disparity of small and extended targets on eliciting perceptions of motion-in-depth. All of their six subjects reported that there was a range of stimulus oscillations of a single dot for which clear motion-in-depth was experienced when a stationary reference (a surrounding random-dot pattern) was present, but when this reference was removed, the dot's motion immediately ceased. Thus, varying relative disparity led to perception of motion-in-depth, but varying absolute disparity did not. Threshold determinations showed that for a single dot this effect amounted to a substantial elevation of threshold (by a factor 2–7) rather than a complete abolition of stereomotion perception. Complete abolition did occur, however, when extended multi-dot-targets were used; i.e. no perception of motion-in-depth occurred when only absolute, unreferenced, changes in disparity were shown. As will be discussed later, these results could not be accounted for by the reduction of effective retinal disparities due to vergence eye movements.

The finding that changes of absolute disparity elicited some weak impression of motion-in-depth of a small, unreferenced target (in agreement with Foley, 1976 and Westheimer, 1979a) but none at all for a multi-dot target, suggested that this difference might be caused by a lateral interaction among the dots. Regan *et al.* (1986) examined this possibility by varying the complexity of the stereogram displays. A multi-dot target display (diameter 28°) with randomly, but more or less evenly spaced dots (dot diameter of 0.3°) was used. A blank annulus of variable width was introduced around a central dot in the multi-dot target display. Two displays of this kind were oscillated in counterphase while each eye viewed one of them. Subjects directed their attention to the central dot; no stationary reference was visible. When the complete display pattern was shown, the central dot did not appear to move-in-depth for any amplitude of counterphase oscillation. The central dot also did not appear to move-in-depth when it was surrounded by a blank annulus with a radius of 0.6°. However, when the radius of the blank annulus was increased beyond 1 to 2° and oscillation amplitude was raised to just below the disparity where fusion broke down, the central dot appeared to move weakly in depth relative to the surrounding dots. (N.B.: the actual positions of the central and surrounding dots were fixed; they never changed relative to one another.) In the limiting case, when only the central dot was visible, the threshold for perceiving motion-in-depth was approximately the same as when it was isolated from the surrounding dots by a blank annulus with a 2° radius.

This experiment produced evidence for a lateral interaction among elements of a display: any apparent motion of a single target, induced by variations of absolute dispar-

ity, was suppressed by the presence of targets, moving coherently, within a distance of 1–2°. Once again, this size is strikingly similar to, what we believe to be, the width of the true Panum's area – the area within which cooperative processes are able to compute differences between absolute disparities of two targets (Fig. 7.2). Conceivably, the differencing process might continue to function to some extent even when a single target is presented, successively, at different absolute disparities, providing that competing targets are not present within the zone of several degrees in which the differencing process operates. The lateral interaction of closely adjacent targets may contribute to the suppression of perceived motion-in-depth induced by vergence eye movements because any residual movement impression, which resulted from such unreferenced changes of absolute disparity, would be suppressed by the coherent motion of the adjacent targets.

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