# BINOCULAR VISION

# 22

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This chapter summarizes current knowledge of the sensory aspects of binocular vision. Previous chapters have covered the anatomic structure and motor control in relation to binocular vision. Here we describe the psychophysical and neurophysiologic contributions to the organization of binocular vision.

The chapter begins with a consideration of the phylogenetic development of a dual visual system. Then the basic geometry of binocular space is described in some detail, as it is not widely understood. The subsequent sections are devoted to the functions of binocular fusion, binocular rivalry, stereopsis, and development of binocularity. In each case the relevant psychophysical and neurophysiologic literature is integrated to provide a complete picture of the topic, and relevant pathologic disturbances of the function are outlined.

## PHYLOGENETIC BACKGROUND

It is remarkable that virtually all animals have two eyes, despite the tremendous variety in general morphology across species (1). Cyclops are essentially unknown outside mythology. Over many types of image-forming capability, from the pinhole eyes of the nautilus, the compound eyes of insects, the pigmented eyespots of the flatworm to the familiar mammalian arrangement, all seem to favor a pairwise organization. Even among invertebrates, the examples of multiple eyes (arachnids, crustaceans) usually consist of two major eyes, with the subsidiary eyes lacking image-forming capability. The reasons for this dominance of binocular vision are difficult to establish but five possibilities suggest themselves:

1. Two eyes may be used to achieve a 360° field of view, since the optics are limited to about 180° (except for compound eyes, which nevertheless always occur in pairs).
2. Where the fields of the two eyes overlap, there is an advantage in detection of faint images and rejection of the optical distortions within the eyes.
3. The second eye could be a safety factor against injury or disease, improving the chance of retaining visual capability when part of the visual field (a scotoma), or the whole eye, is damaged.
4. The presence of two mobile eyes allows the organism to converge the line of sight on distant objects and obtain a reading as to their absolute distance.
5. Probably the most dramatic reason for binocular vision is to achieve **stereopsis**—the ability to use binocular disparities to perceive distance in the third dimension of visual space.

Presumably all animals develop a visual system with some weighting among these different factors. Most lower animals take advantage of the possibility of a 360° field of view by having the eyes pointing in opposite directions. This applies to fish, many birds, and to a large extent in mammals which are preyed upon. On the other hand, most predatory animals, from spiders and crustaceans through birds to mammals and humans, tend to have the eyes facing in the same direction. This is, presumably, to take advantage of stereopsis, since behavioral stereoscopic depth perception has been demonstrated in humans (2), monkeys (3), cats (4), and falcons (5) and is likely to be widespread across other species.

Actually, almost all animals show some de-

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gree of binocular overlap, even those with a full 360° field (1). The binocular overlap is almost exclusively in the forward direction (although it may be directed upward or downward in different species). However, it is unclear whether the binocular field is used to take advantage of stereoscopic depth cues or merely for the improvement in image reliability by binocular comparison. Certainly most birds have a region of improved visual acuity in the binocular segment, in addition to the laterally directed monocular foveae. They, therefore, probably have sufficiently good visual acuity to use binocular disparity cues for stereopsis (Fig. 22–1).

The relative importance of convergence as a primary cue to distance may be assessed by noting that many species have little or no convergence. This is true for many birds and, in particular, the owl, with its large binocular fields (6). A similar situation occurs in lemurs. This would suggest that convergence is utilized mainly to optimize the alignment of the retinas for the assessment of binocular disparities for stereopsis rather than as a primary cue to distance. This does not exclude the possibility that some animals use the minimization of disparity in the binocular segment to determine the distance of an object on the basis of muscular convergence information.

In addition to the benefits of binocular vision, any animal with two eyes obtains the advantage of duplication against dysfunction, but if this were a major advantage, a further proliferation of the number of eyes might be expected. More than two eyes with image-forming capability is essentially unknown, and two or four median eyes that develop embryologically in the elasmobranch atrophy before adulthood (1). The advantage obtained against dysfunction is, therefore, probably of minor importance.

We are left with the conclusion that the major reasons for binocular vision are probably to achieve a large visual field and to enable the use of stereoscopic depth perception, which is discussed in detail in a later section.

## SENSORY ASPECTS OF BINOCULAR VISION

Assuming that the eyes are aligned binocularly on the stimulus field, there are several sensory aspects of binocular vision which arise from different configurations of stimulus details.

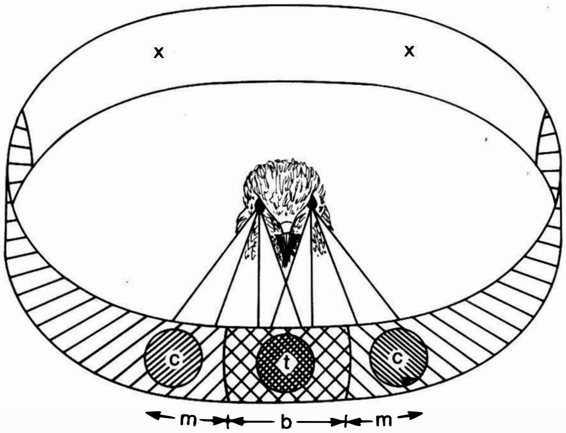


FIG. 22–1. Projection of the three regions of high acuity in the visual field of a hawk. The central fovea (c) project to two monocular regions, while the temporal foveae (t) project to a binocular region. In the case of this species a rear portion of the field is out of view (x). (Walls GL: The Vertebrate Eye. New York, Hafner, 1967)

**1. Visual direction.** A stimulus point can fall on retinal regions that are exactly corresponding in the two eyes. The point will be seen as being in the same visual direction whichever eye views the stimulus. The question of perceived visual direction involves extensive consideration of monocular vision and eye movements, so the discussion here will be limited to binocular correspondence. Departures from correspondence in the form of small differences between the image positions in the two eyes are termed binocular disparities.

**2. Sensory fusion.** If the image on one eye is moved very slightly to produce a small **binocular disparity** in visual direction, the binocular image will still be seen as a single image. The range of disparities for which fusion occurs is known as **Panum's area.** Beyond this region images are seen doubled or in **diplopia.** When the images are fused, there is some degree of binocular summation of the energy in the two images.

**3. Dichoptic stimulation.** If the images in the two eyes are very different, or if they derive from the same stimulus but are shifted, rotated, or magnified so that dissimilar contours are present in the same retinal area, then a binocular rivalry will be set up between the two monocular images. If one eye is strongly dominant as a result of either stimulus characteristics or organismic variables, perception of the image in the other eye may be entirely absent due to interocular suppression.

4. **Stereopsis.** If the binocular disparity has a horizontal component, the point will be seen in vivid depth nearer or farther than the point of fixation, within some range of limiting conditions. Depth is perceived in the region of both fusion and of diplopia.

These four aspects of binocular vision will form the major subdivisions of the subject. A final section considers the development of binocularity in the visual system.

## VISUAL DIRECTION AND THE HOROPTER

**Corresponding retinal points.** In the analysis of binocular space perception, the relative distance of objects from the observer is determined in general by the binocular disparity between the images falling on the retinas of the two eyes (in conjunction with the convergence of the eyes).

It is necessary to define more precisely the concept of corresponding points having zero binocular disparity on the two retinas. The simplest definition is based on ocular geometry (Fig. 22–2), in which corresponding points on the two retinas are defined as being at the same horizontal and vertical (or monocular visual direction) from the center of the fovea of each eye. (The rotation of the eyes must be taken into account, but may be considered identical when the eyes are in the primary, straight-ahead position.)

Specific to every position of binocular fixation, there must be a set of points in space for which the binocular disparity is zero, so that the points are in the same visual direction in space. The locus of points that have zero binocular disparity is known as the **horopter** (the "horizon of vision"), a term introduced by Aguilonius (7). The **point horopter** is in general simply a line in space passing through the point of fixation, although in certain restricted circumstances it may become a two-dimensional surface.

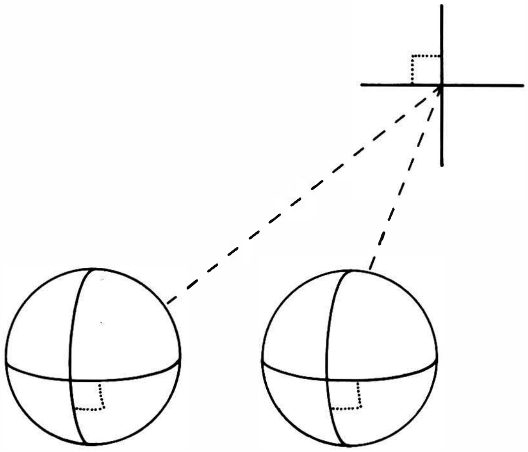


FIG. 22–2. Geometric retinal correspondence. When the eyes are aligned and viewing at infinity (shown here in perspective), a point at a given distance vertically and horizontally away from the fixation point projects equivalent distances horizontally and vertically away from the fovea in the two eyes. These two points are then in geometric correspondence.

Points that are in geometric correspondence on the two retinas do not necessarily project physiologically to a single point of binocular combination in the primary visual cortex. While it is generally true that corresponding points in the retinas project to the same region of visual cortex, there are two important ways in which a precise relationship does not hold. The first is that many neurons in the primary visual cortex respond best to stimuli with some nonzero binocular disparity (8). This makes the physiologic definition of zero disparity a statistical question of the distribution of optimal disparities, rather than a precise correspondence.

**Types of horopter.** The definition of the horopter used thus far has been purely geometric and based on the concept of binocular retinal correspondence with zero binocular disparity. This geometric horopter must be distinguished from the empirical horopter measured on a given observer, which may deviate from the geometric construction if there is some empirical deviation from the linear geometric definition of corresponding points. The empirical factors might include distortions in the physiological correspondence between the two retinas and optical distortions in the ocular media.

Furthermore, in extending the horopter concept to perception of objects in space, it is possible to define a horopter based on perceived distance from the observer, rather than on binocular disparity *per se*. This is a higher-level percept involving more of the perceptual apparatus, which may add compensations or distortions to the form of the binocular correspondence horopter. The distance horopter is therefore not as fundamental a concept as the binocular correspondence horopter. Two criteria for distance horopters have been used. Setting stimuli at equal apparent distances from the observer at different eccentricities defines the equidistance horopter, whereas setting stimuli so as to appear in the frontoparallel plane defines the frontoparallel horopter. However, a fuller description of the distance horopters is beyond the scope of this chapter.

A special case of interest involves the use of disparities in only the horizontal direction, since it is only these disparities that are involved in depth perception. This is equivalent to a horopter measured with vertical lines, and is therefore known as the longitudinal horopter by analogy with the vertical lines of longitude on the globe of the earth. The longitudinal horopter is the one most commonly specified in texts and is the main one to have been measured empirically. It is important to note that whereas the point horopter (measured using points as stimuli) is limited to a single line in space, except for fixation at infinity, the longitudinal horopter (measured using vertical line stimuli) is a curved two-dimensional surface in space.

A final type of horopter, which is an extension of the empirical horopter, may be specified as the locus of points in space which appear binocularly fused to the observer. The fusion horopter is a three-dimensional volume in space extending around the horopter. The fusion horopter is the one preferred in ophthalmologic practice.

**History of the horopter.** The concept of corresponding visual directions and the double vision arising from a noncorrespondence was recognized by Euclid and Leonardo. Aguilonius (7) was more specific in postulating the existence of a surface in which single vision occurred, the earliest attempt to describe the fusion horopter. The longitudinal horopter in the horizontal visual plane was first defined by Aguilonius (7) as a circle passing through the optical centers of the two eyes and the point of fixation, as shown in Figure 22–3 (this construction is usually attributed to Vieth (9) and subsequently Müller (10). All this analysis preceded the realization that binocular disparity away from the horopter led to depth perception, which was first demonstrated in 1833 by Wheatstone (11).

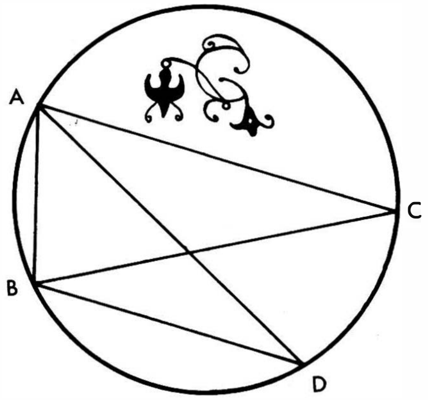


FIG. 22–3. Vieth-Müller circle from an early diagram by Aguilonius, passing through the point of fixation (**C**) and the nodal points of the two eyes (**A,B**). All points on such a circle subtend an equal angle at the eyes. Therefore, since the eyes are converged at this angle to foveate at the fixation point, all other points on this circle (*e.g.*, point D) must be in geometric correspondence.

An initial description of the form of the horopter outside the horizontal plane was developed by A. Prévost (12), who pointed out that it consisted of a single vertical line. The full specification of the geometric form of the point and line horopters was elaborated by Helmholtz (13) and concurrently by Hering (14). It was incorrectly considered to be a toroidal surface by Serre (15), Linksz (16), Fry (17), and Shipley and Rawlings (18). Other workers have tended to ignore the question of the horopter away from the horizontal visual plane, and usually written as though the point horopter were a two-dimensional surface (19,20). The most recent theoretical derivation (21), while correct in most respects, essentially reiterates the work of Helmholtz more than a century ago.

Empirically much work has been done on the measurement of the longitudinal horopter, beginning with Hering (14) and Hillebrand (22), who found a consistent deviation from the geometric horopter. Until recently no measurements have been made away from the horizontal plane of either the longitudinal or point horopters, so that the degree to which the two-dimensional geometric specification is empirically valid is unknown. Current work (23) suggests that the geometric specification is formally valid, although quantitative details may need to be modified. Within the horizontal visual plane the longitudinal horopter, the fusion horopter, and the effects of eccentric fixation have been studied in detail by Ogle (24).

**The point horopter with symmetric fixation in the visual plane.** To introduce the basic form of the point horopter, a simplified case will be considered with only symmetric fixation in the visual plane. In this position eye torsion may be considered to be zero. Retinal correspondence will be defined geometrically and optical aberrations will be assumed to be absent.

When the observer converges symmetrically at points closer than infinity, there is another consequence of significance concerning points away from the horizontal or vertical axes. As shown in Figure 22–4, it is generally the case that off-axis points project to the two retinas with both horizontal and vertical disparities. The only exceptions are when a point is at infinity, when it would have no disparity, and when the point is at the distance corresponding to the horopter, which would nullify the horizontal disparity. But note that the vertical disparity is produced because off-axis points are necessarily nearer to one eye than the other, with a resulting difference in magnification of the projection angle in the two eyes (Fig. 22–4). Thus, all off-axis points (except at infinity) project with some vertical disparity to the two eyes, and can therefore never be included in the horopter.

The result of the exclusion of off-axis points is that even for symmetric fixation in the visual plane the point horopter is limited to a one-dimensional set of points in the vertical and horizontal meridians of the two eyes, except for parallel fixation at infinity, as demonstrated in 1843 by A. Prévost (12). Geometrically, the disposition of the set of points in the vertical meridian will be a vertical straight line passing through the fixation point in space.

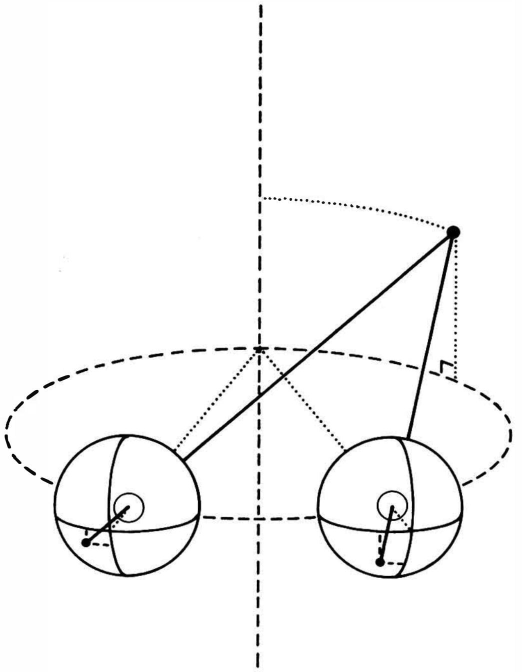


FIG. 22–4. For convergence at any distance other than infinity, all points that do not lie on the Vieth-Müller circle or the vertical horopter line project to the retina with either a vertical disparity or both a vertical and horizontal disparity. **Dashed lines** show geometric horopter for symmetric fixation. **Dotted lines** are construction lines. **Full lines** represent relevant light rays. The vertical disparity arises from the differential magnification occurring when the point is closer to one eye than the other, as must occur with all points off the vertical axis. The three-dimensional point horopter is therefore not a surface, but two lines in space.

At the same time, there is another component of the symmetric line horopter corresponding circle designated as the Vieth-Müller circle (although it was first specified by Aguilonius [7]). The Vieth-Müller circle passes through the point of fixation and the nodal points of the two eyes, since in this circle all points on the circumference make equal angles between the two nodal points and therefore equal disparities on the retinas. All other points in space project with some horizontal or vertical disparity to the two eyes. The point horopter for symmetric fixation in the visual plane therefore consists of a vertical line and a horizontal circle (see Fig. 22–4).

**The point horopter with asymmetric convergence in the visual plane.** Asymmetric

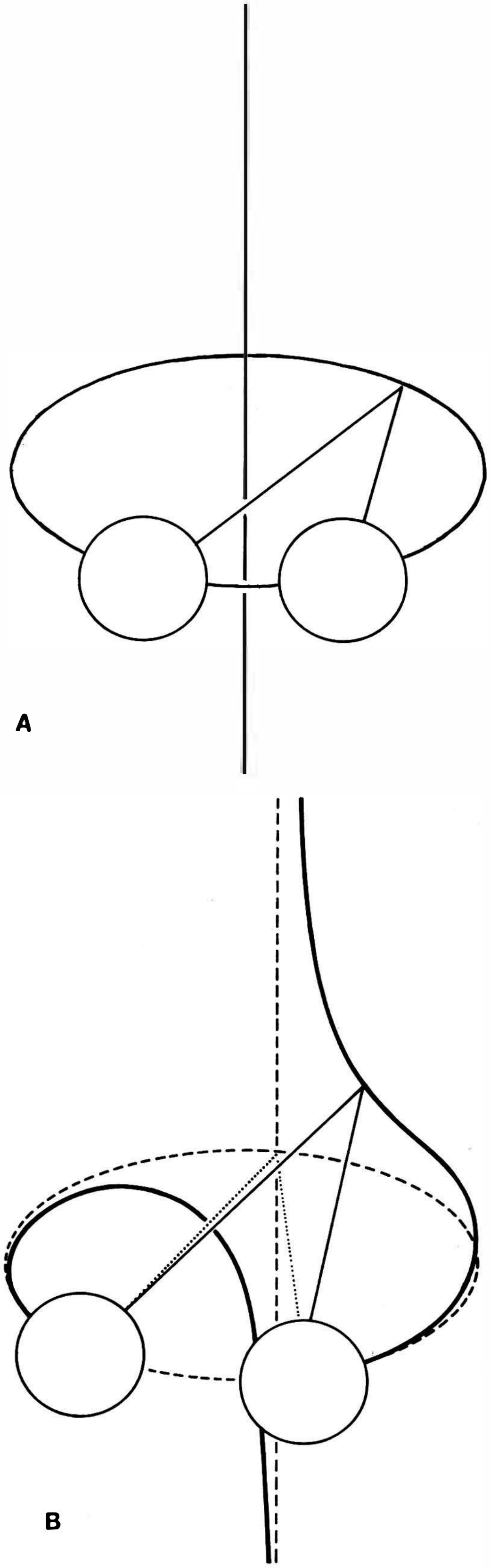


FIG. 22–5. A. Geometric horopter with asymmetric fixation. Note that both the Vieth-Müller circle and the vertical horopter line remain fixed in space as fixation moves around Vieth-Müller circle. B. Geometric horopter with asymmetric fixation away from both horopter lines. Horopter (**full line**) becomes a one-turn helix winding around the symmetric horopter (dashed **line**).

convergence is an important consideration, not only for its occurrence in normal viewing situations, but also because in many respects it is equivalent to symmetric fixation with a unilateral image magnification (aniseikonia), such as occurs in anisometropia and unilateral aphakia. The simplest case of asymmetric convergence away from the vertical meridian is within the horizontal visual plane assuming no eye torsion. Here the same logic that generated the Vieth-Müller circle would imply that as the eyes fixate at different points around a given Vieth-Müller circle, the horizontal horopter always falls on the same circle.

Furthermore, the vertical line component of the horopter also remains essentially fixed in space directly in front of the observer as the eyes are moved around the Vieth-Müller circle, rather than following the position of the foveas (Fig. 22–5A). This occurs because the difference in image magnification away from the vertical meridian is a function of the distance of the image from each eye, which is essentially unaffected by ocular rotation (except that the center of rotation differs slightly from the nodal point of the eye). Thus in gaze to the left the foveal image in the left eye is magnified relative to the right eye image, and the magnification is equal only for the vertical meridian directly in front of the head, which projects to a peripheral line on the retinas (as shown in Fig. 22–4). The immediate consequence of this geometry is that the regions immediately above and below the fovea have an inherent vertical disparity in eccentric fixation which must affect the stereoscopic and fusion abilities (see Fig. 22–12).

**The generalized point horopter in asymmetric convergence.** Finally, the most general case with respect to fixation is to allow fixation at any point, which in general will include asymmetric convergence away from the visual plane. This case was developed in detail by Helmholtz (13) and is a curve of the third degree which forms a single loop spiral (Fig.

22–5B). This curve may be construed as the geometric result of stretching the line and circle horopter so as to pass through the point of asymmetric fixation. Thus, the generalized helix of the point horopter is constrained to pass through the point of fixation, and the nodal points of the two eyes, and to become asymptotic to the vertical line at ± ∞.

The value of projecting the horopter line onto an abstract cylinder in space is that it allows dissociation of the effects of ocular rotations from the inherent disparity constraints. Ocular cycloversions and cyclovergence tilt the entire cylinder, without affecting the mapping of the horopter line onto the cylinder.

## EMPIRICAL EVIDENCE FOR THE HOROPTER

**The Visual Plane.** As mentioned previously, the measurements of the visual plane by Hering (14) and Hillebrand (22) (which have been made only within the visual plane) showed a consistent deviation from the geometric Vieth-Müller circle, whether the horopter is measured in terms of equal visual direction or by the more perceptual criteria of the range of fusion or equal perceived distance.

Ogle (19,26) showed that the empirical horopter in the visual plane is well described by a curve from the mathematical class of conic sections, which would imply that it is either a circle, ellipse, straight line, or hyperbola, depending on the radius of curvature at the point of fixation. If the Hering-Hillbrand deviation from the Vieth-Müller circle is a fixed amount of retinal disparity at each angle of eccentricity, then the form of the horopter will change with fixation distance. (It is only when there is no deviation from the Vieth-Müller circle that the horopter will remain a circle as fixation distance varies.) A family of curves for different fixation distances is shown in Figure 22–6, illustrating how the empirical horopter progressively curves away from the observer as fixation distance increases.

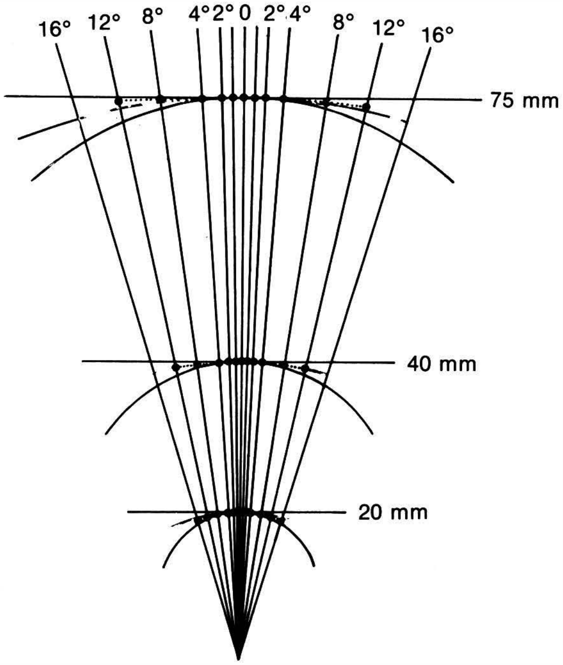


FIG. 22–6. Hering-Hillebrand deviation from the geometric horopter circle. Note the change in form of the deviation with fixation distance, although the retinal disparity maintains a fixed deviation from geometric correspondence. (Ogle KN: Researches in Binocular Vision. Philadelphia, Saunders, 1950)

**Fixation at infinity and shear of vertical meridians.** The simplest case of all is the geometric point horopter when fixation is at optical infinity. Here rays from each point of the frontal "plane" of infinity are parallel, and this is therefore the only case where the point horopter can be considered a plane. However, there is already a complication. Volkmann (25) and Helmholtz (13) compared the vertical meridian between the two eyes and found that with fixation in the primary position there is a tilt of approximately 2° when the vertical of one eye is matched to the vertical in the other, whereas no such tilt appears in the horizontal direction. Since this tilt is anisometropic to the vertical direction, it is best described as a shear of retinal correspondence.

The Helmholtz shear completely alters the plane of the empirical point horopter from the geometric constrict. Figure 22–7A shows the projection of the vertical correspondence meridians of the two eyes through the pupils with parallel symmetric fixation. Each set of projection lines form a plane in space, and the intersection of these two planes defines the horopter for the vertical midlines. It immediately follows from the 2° tilt of the vertical midlines that the line in which the planes meet will vary in angle according to fixation

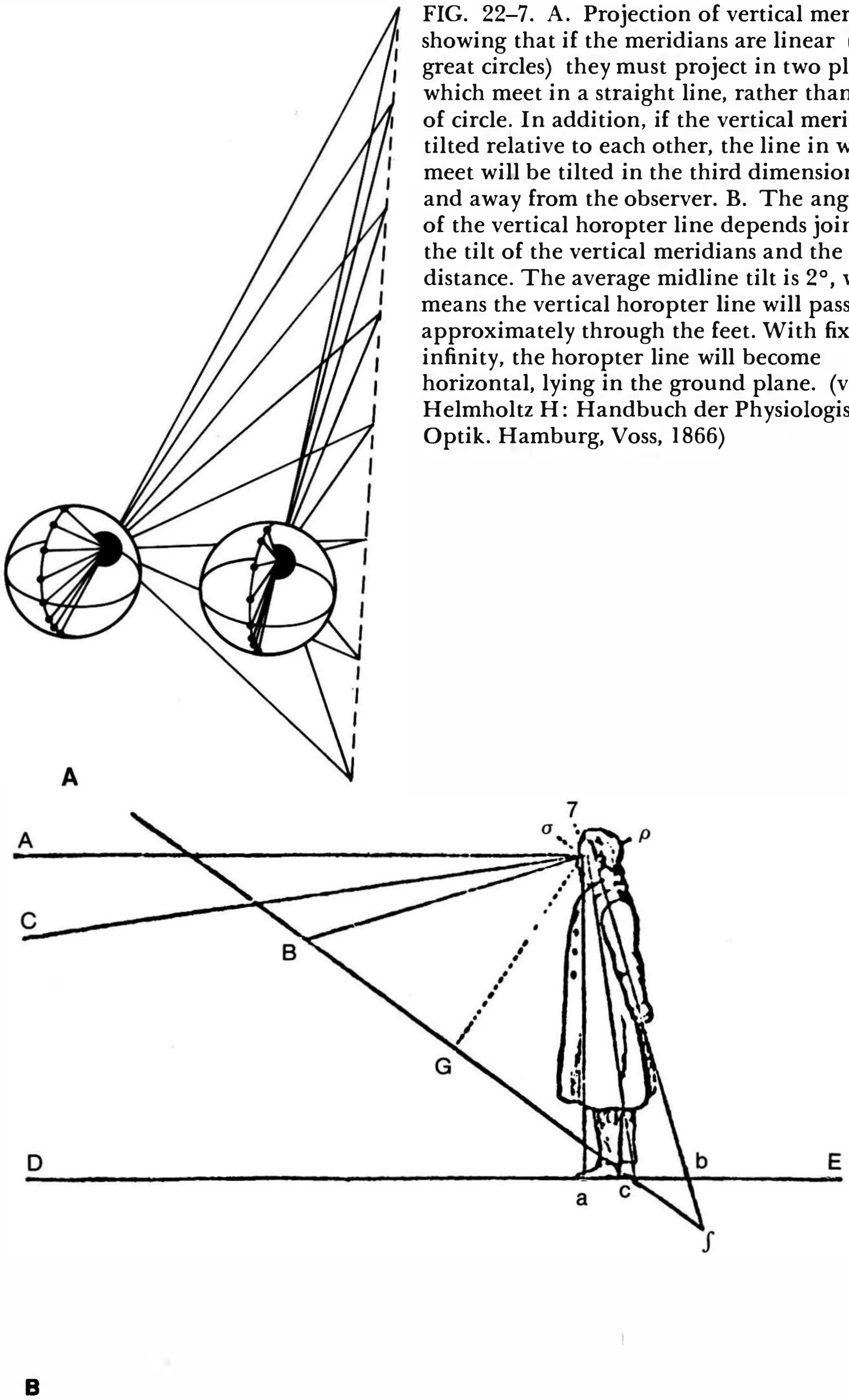


FIG. 22–7. A. Projection of vertical meridian, showing that if the meridians are linear (*i.e.,* great circles) they must project in two planes which meet in a straight line, rather than any kind of circle. In addition, if the vertical meridians are tilted relative to each other, the line in which they meet will be tilted in the third dimension toward and away from the observer. B. The angle of tilt of the vertical horopter line depends jointly on the tilt of the vertical meridians and the fixation distance. The average midline tilt is 2°, which means the vertical horopter line will pass approximately through the feet. With fixation at infinity, the horopter line will become horizontal, lying in the ground plane. (von Helmholtz H: Handbuch der Physiologische Optik. Hamburg, Voss, 1866)

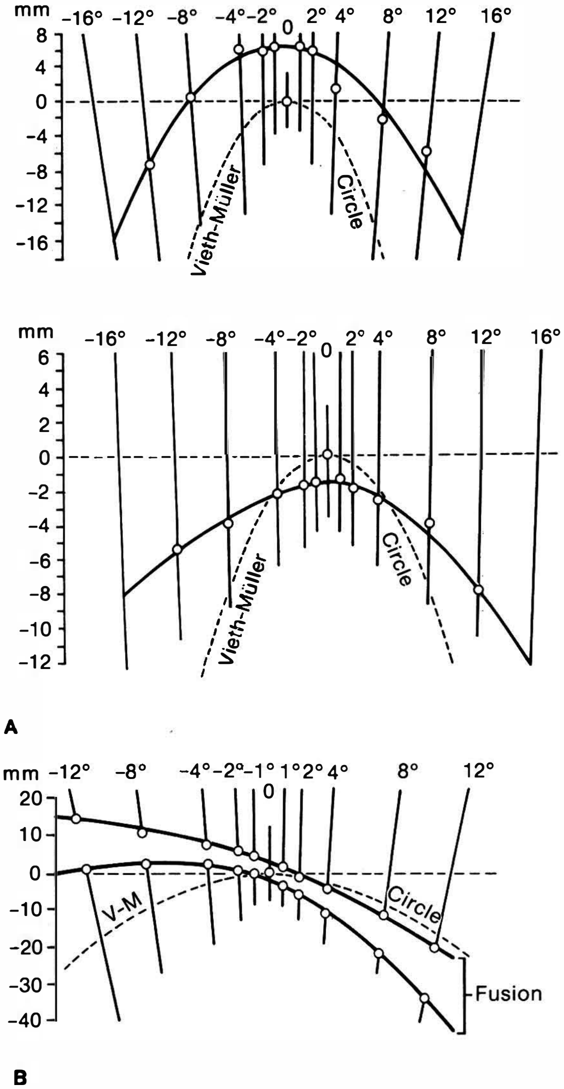


FIG. 22–8. A. Effect of fixation disparity on the position of the horopter circle. **Upper:** exodeviation. **Lower:** esodeviation. B. Effect of aniseikonia (differential magnification of image in the two eyes) on the form of the horopter circle, which becomes an ellipse. (Ogle KN: Researches in Binocular Vision. Philadelphia, Saunders, 1950)

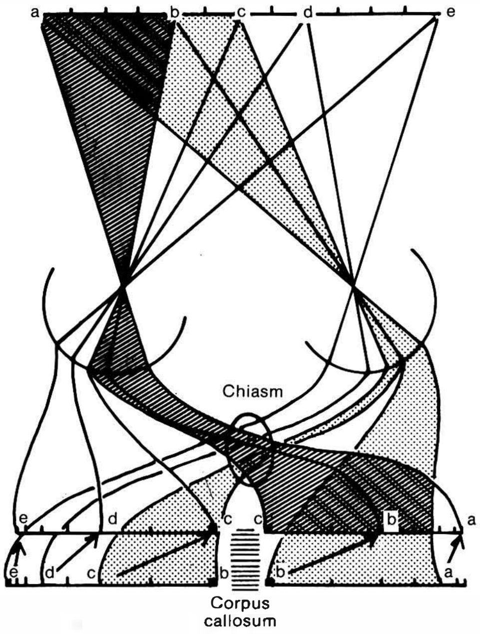


FIG. 22–9. Diagram of neural connections in anomalous retinal correspondence (ARC). Equally spaced points a, **b**, **d**, and e around point **c** in visual space project through the nodal points of the eyes onto the retinas. Note that the projection onto the cortex gives preferential weighting to the foveal region (point c). Development of ARC in strabismus gives distorted match of left to right connections from left and right eyes. Region a **b** c from the left eye (**stippled**) has anomalous connection relative to region a **b** c from the right eye (**hatched**).

distance (Fig. 22–7B). For fixation at infinity, the planes will meet in a horizontal line running below the eyes, roughly in the plane of the ground when the observer is standing. For parallel fixation on the horizon, all other meridians of the eyes will also project into the same plane, so the plane of the point horopter will coincide with the entire plane of the ground extending to the horizon. Helmholtz therefore suggested that the 2° shear has an adaptive function of removing the horopter from correspondence of the stars to the plane of the ground in which are located many of the objects that are of survival value to the human organism.

**Binocular abnormalities and the horopter.** We shall consider three binocular abnormalities which affect the form of the horopter: fixation disparity, aniseikonia, and abnormal retinal correspondence.

**Fixation disparity** is a very straightforward concept, and simply means that the observer is fixating binocularly with a slight disparity either in front of or behind the plane of the stimulus. Typically, one eye will fixate the object directly with the central fovea, while the other eye will fixate slightly eccentrically, producing the fixation disparity. This may arise from a small foveal scotoma or from an oculomotor imbalance which is tending to pull the eyes away from the appropriate angle of convergence. The effect on the horopter is the same in either case. The horopter simply passes through the actual point of fixation rather than through the fixation stimulus. An example of a horopter showing fixation disparity was obtained by Ogle (19) on his own eyes (Fig. 22–8A).

**Aniseikonia,** the unequal magnification of images in the two eyes, occurs principally as a result of unequal refraction in the two eyes (or even unilateral aphakia). When the refractive error is corrected, there may be a residual difference in the magnification of the two images. This difference distorts shape of the entire horopter, and the distortion may become so large that binocular fusion and stereopsis become impossible.

The form of the horizontal plane of the empirical fusion horopter with 3% magnification of the image to the right eye (26) is shown in Figure 22–8B. The curvature of the horopter now has a backward tilt to the left. As a quantitative example, at an observation distance of 1 m, a magnification difference of only 5% will product a tilt of as much as 50°, which may make normal binocular fusion and stereopsis very difficult, and even lead to strabismus and amblyopia. In fact, Peters (27) found a loss of stereopsis when artificial aniseikonia was produced with a magnitude as little as 1 diopter difference in refractive power between the two eyes.

**Anomalous retinal correspondence (ARC)** is a condition that occurs in certain types of strabismus, wherein equal visual direction (correspondence) as established for certain retinal regions which are disparate in normal vision. Consider the case of concomitant esotropia with the visual image symbolised by the line a b c d e. The region ab projects to the same (right) visual cortex as does the fixing left eye, and the region cd projects to the same (left) visual cortex as does the fixing left eye (Fig. 22–9). While not in the exact corresponding areas, these projections of the left eye can potentially reconnect with the normal cortical areas (the arrows in Fig. 22–9). (In fact, the reconnection is perhaps at a higher level of processing, but the concept is the same.) This adaptation is called anomalous retinal correspondence (ARC). The region cb in one eye can potentially reconnect to the other eye's image region: 1) through the corpus callosum, and 2) by means of nasotemporal overlap. However, it is doubtful whether there is development of ARC to complete the horopter in this anomalous region (28). Furthermore, there is no evidence that any form of stereopsis develops in the anomalous region.

One important feature of early esotropia is a profound suppression of the perception from the central region of whichever eye is not fixating. This probably arises from the anatomy. The representation of the retina on the cortex is not linear; the central retina is greatly magnified. Lateral interconnections in visual cortex are of similar size, but whereas a 1 mm region of cortex will process a few seconds or minutes of arc of the visual field near fixation, it will process several degrees of visual field in the periphery (Fig. 22–9). The stretch from b (right eye) to b (left eye) is a long one in the cortex, although it is a small one in angle of vision. The adaptation is a difficult one here, and the interconnection is often not made, and suppression of one image results. However, the stretch from a to a, and from d to d is shorter in the cortex, and function can continue. Thus, one often finds suppression of the central visual field with maintained binocularity for motor fusion and stereopsis in the peripheral visual field in esotropic cases of moderate amounts. Where the strabismus angle is extremely large, reconnection may be impossible anywhere in the cortex. Suppression is then the adaptation everywhere. ARC and suppression are adaptations that are not possible in adult visual cortex. When the onset of strabismus is later than about 6 years of age, diplopia persists.

## BINOCULAR FUSION

### CLASSIC THEORIES OF BINOCULAR FUSION

There have been four classic approaches to the binocular fusion of stimuli in the two eyes into a single percept: the synergy hypothesis, the local sign hypothesis, the eye movement hypothesis, and the suppression hypothesis. Each is subject to serious misgivings, and all four have essentially been rendered obsolete by neurophysiologic data on binocular responses of cortical neurons, which give rise to a fifth, physiologic hypothesis. Since elements of several of the classic hypotheses are incorporated into the physiologic hypothesis, they will be briefly described.

In the synergy hypothesis, Panum (29) originated the suggestion that binocular fusion is due to the "binocular synergy of single vision by corresponding circles of sensation." By this he appeared to mean that the stimulus in one retina could be physiologically fused with a range of similar stimuli around the point of precise correspondence in the other retina. This range is now known as **Panum's area.** Nevertheless, information as to which point within the "corresponding circle of sensation" is stimulated is not lost, but remains available in the visual system for the perception of depth. This last stipulation is necessary because, while the range of binocular disparities allowing fusion is typically in the region of 10–20 arc min, stereoscopic depth may be perceived from a disparity 100 times smaller.

The problem with the synergy hypothesis is that it seems contradictory that the positional information within the region of the corresponding circle of sensation is simultaneously lost for fusion and yet available for stereopsis. In this sense, Panum's hypothesis does not progress much beyond a description of the data.

The local sign hypothesis was first applied to stereopsis and binocular fusion by Hering (14). The essence of this hypothesis is that when any point on the retina is stimulated, information as to its position is coded as a "local sign" (or what computer users call an "address") as to where the stimulation occurred. As in the synergy hypothesis, there is a small range of binocular disparities for which the local sign is identical, and therefore the image is seen as single. The finer resolution of stereoscopic depth is treated by positing a further "depth sign" which codes the precise binocular disparity information separately from the lateral sign information.

The difficulty with the local sign hypothesis is that it does not explain the occurrence of rivalry between dissimilar forms projected to corresponding points in the two eyes (13). For example, a dot to one eye may fall in precise correspondence with one part of a line to the other eye. Fusion is not obtained, but rather there are rivalry and suppression between the dot and line in the region of correspondence. This is contradictory to the local sign hypothesis, since each stimulus should have the same local sign at this point and therefore be perceived as fused.

As an alternative, Helmholtz (13) proposed an eye movement hypothesis of fusion, based on the idea that small eye movements made the image so unstable that accurate specification of stimulus position was impossible within some range. This range corresponded to the region of fusion by virtue of positional confusion.

The eye movement hypothesis of fusion is immediately invalidated by the fact of the much finer resolution of stereoscopic depth, which should imply a similar resolution for fusion.

Lastly, the suppression hypothesis builds on observations that dissimilar stimuli in corresponding retinal regions of the two eyes tend to produce reciprocal suppression in perception, resulting in rivalry of alternate perceptions of one or the other stimulus, but not both. Developed in an early form in the 18th century by du Tour, this hypothesis was more recently revived by Verhoeff (30). Fusion is explained as alternating suppression between the two monocular images, resulting in the perception of a single image.

What is ignored by the suppression hypothesis is that alternation between two positions would produce a perception of apparent motion or displacement of the stimulus from one position to the other. No such displacement is observed in fused disparate images. Thus, while interocular suppression undoubtedly occurs in many situations where one eye is dominant or the two are in alternating rivalry, it cannot provide an explanation for fusion.

The conclusion to be reached is that, though each hypothesis may have some degree of validity in special circumstances, none provide a complete explanation of sensory fusion, one of the most compelling phenomena of binocular vision.

## PHYSIOLOGIC BASIS OF FUSION AND DIPLOPIA

An appropriate resolution of the controversy over fusion arises from consideration of the physiologic basis of binocularity in the visual cortex, as suggested by Roenne (31). An initial version of the physiologic hypothesis is based on the distribution of disparities of the binocular receptive fields (32). In its current form this hypothesis would utilize the neuro-

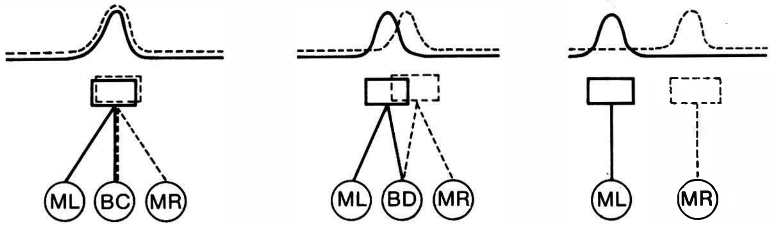


FIG. 22–10. Model of binocular fusion and diplopia considered from the point of view of four classes of cortical neuronal receptive field with similar visual directions—monocular left eye **(ML)**, monocular right eye **(MR)**. binocular corresponding **(BC)**, and binocular disparate **(BD)**. Stimulus inputs to these receptive fields are shown as **full** (left eye) and **dashed** (right eye) **lines;** for zero, small and large binocular disparities.

physiologic data on different types of binocular neurons in the visual cortex. Hubel and Wiesel (33) showed that one set of neurons in cat cortex could be driven by stimulation of an appropriate region of either eye (binocular neurons), whereas there were two further sets of neurons that would be activated only by stimulation of a single eye (monocular neurons). In addition, several groups of investigators (8,34) have found that while some binocular neurons had receptive fields at exactly corresponding points on the two retinas, others showed a preference for fields with various degrees of binocular disparity away from exact correspondence, not only in the horizontal plane but in all retinal directions. The extent of binocular interactions and their interpretation of these disparities as the basis for stereoscopic depth perception is discussed in the stereopsis section, but the relevance for the theory of binocular fusion is hard to dispute.

Thus, neurophysiologically we may define four classes of neurons having binocular corresponding, binocular disparate, monocular right, and monocular left excitatory receptive fields (Fig. 22–10). Presumably, each neuron is "labeled" as deriving stimulation from a specific visual direction. The visual direction is unambiguous for all classes except the binocular disparate, where we shall assume that it falls midway between the visual directions of the two monocular receptive fields for that neuron. To complete the neurophysiologic framework, we shall assume that binocular interactions with simultaneous stimulation of both eyes are negligible for the present purposes.

Now consider the aggregate of neuronal responses as stimuli to the two eyes are presented on corresponding points and then moved gradually away in disparity until fusion breaks and diplopia is perceived. When the stimuli are in corresponding points, the three classes (binocular corresponding neurons and monocular right and left neurons) derived from a single visual direction are stimulated. Since all three types have the same visual direction label, there is no conflict and the stimulus, encoded as the sum of all neurons responding, is seen as single.

When a small disparity is introduced, some binocular disparate neurons are stimulated, and the binocular corresponding neurons should cease responding. But now the monocular right and monocular left neurons are each stimulated for a visual direction slightly to either side of the mean visual direction for the binocular disparate neurons (Fig. 22–10). Thus, the two monocular visual directions, which would be discriminably different if presented singly, are integrated with a third set of responses from the binocular disparate neurons. There should, therefore, be a range of small disparities for which the binocular response gives a unitary perception of a fused stimulus.

Finally, the disparity is increased beyond the range where the binocular response can be integrated with the two monocular responses. Now each monocular response is associated with a different visual direction, and therefore two separate stimuli are perceived in diplopia.

What happens to the visual direction associated with the binocular disparate neurons is a current issue. No ghost image is seen between the diplopic images when the disparity is large. It is possible that no visual direction was assigned in the first place, or that there is suppression of the visual direction of the disparate neurons by the monocular excitatory neurons. However there is a more likely explanation. As discussed more fully under Stereopsis, the binocular disparate neurons probably operate in a small range, essentially only in the region of fusion. Larger range disparities do not stimulate these neurons, so that the question of their visual direction would not arise when the disparities are beyond Panum's area.

## EMPIRICAL EVIDENCE

### Retinal Eccentricity, Fusion, and Cyclofusion

Binocular fusion of similar contours does not have a constant limit, but varies as a function of spatial position on the retina. The variation in fusion limit as a function of eccentricity (24) is shown in Figure 22–11A. Thus, "Panum's area" is not of fixed size, but increases roughly in proportion to distance from the fovea.

This increase in fusion limit is adaptive from three standpoints. One is that the size of retinal receptive fields and, hence, visual acuity both show a corresponding proportion change with eccentricity. It is appropriate for the size of Panum's area to be matched to the monocular grain of the retina at that point.

The increase in Panum's area is also adaptive in terms of the binocular environment. Figure 22–11B shows the disparities produced by binocular viewing of a plane optimally tilted at the angle of the vertical horopter at a distance of 20 cm. This situation might be approximated by a person reading a book or other flat material at a comfortable distance. The disparities present at large distances from the foveae are substantial, and increase roughly in proportion to degree of eccentricity. A corresponding increase in Panum's area, therefore, allows a much larger region of such a plane to appear fused than would otherwise be the case.

The third reason why it is helpful to have fusion increasing with eccentricity is that it allows a degree of sensory cyclofusion. If Panum's area remained constant at all eccentricities, then the maximum interocular orientation difference between two lines that would remain fused would be only about 4′ for a line across the full extent of the retina, such as the horizon. As it is, the increase in Panum's area at large eccentricities allows fusion of orientation differences of as much as 2° in theory (19). In practice, the extent of cyclofusion depends on the stimulus size and configuration (35), as does the extent of Panum's area itself (36).

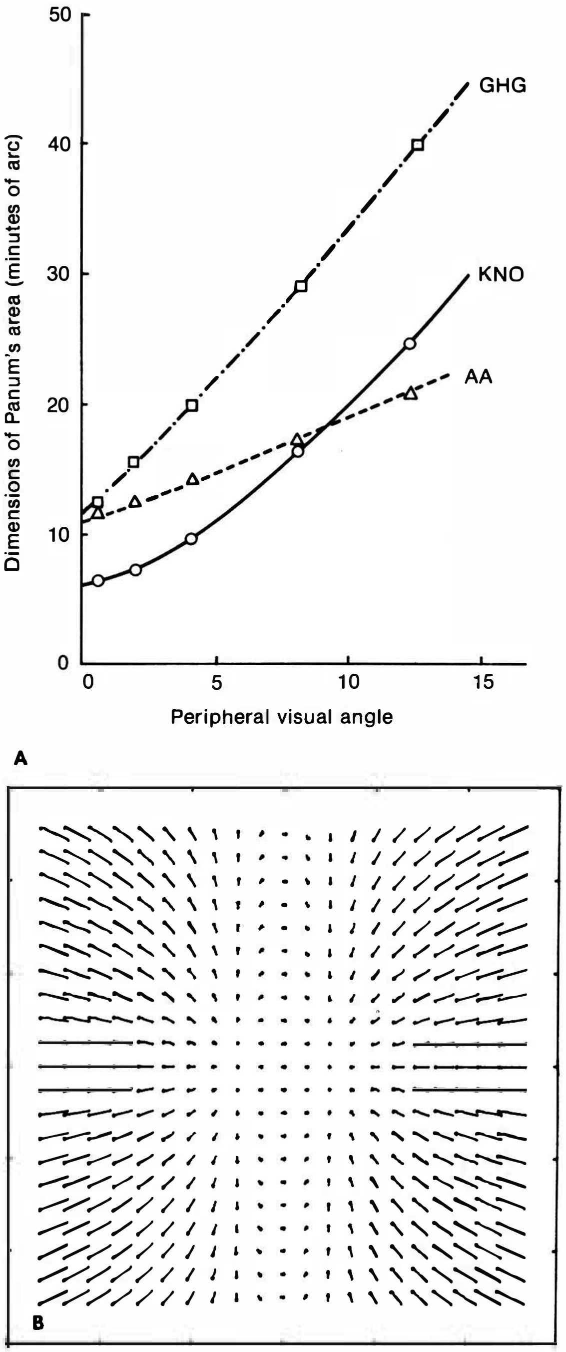


FIG. 22–11. A. Variation in Panum's area of binocular fusion with retinal eccentricity. (Ogle KN: J Exp Psychol 44:253–259, 1952. Copyright 1952 by the American Psychological Association. Reprinted by permission) B. The field of geometric disparities of a flat plane viewed at 20 cm and slightly in front of the fixation point. This shows that relatively large disparities can occur in peripheral regions under conditions that might occur while reading or writing. (Nakayama K: Proc SPEI 120:2–9, 1977)

## Fusion Horopter

As an application of this idea of the range of sensory fusion, one can obtain the range of fusion around the horopter of corresponding points to show the total region of space before the observer for which point stimuli will appear fused. This empirical fusion horopter is depicted in Figure 22–12 for the special case of symmetric fixation in the visual plane (a) and the general case of asymmetric fixation off the visual plane (b). Note that the fusion horopter runs wide of the geometric Vieth-Müller circle due to the Hering-Hillebrand deviation. The case for asymmetric fixation is based on the Helmholtz one-turn helix described in a previous section. The narrowing of Panum's area near fixation produces the thinning of the fusion horopter in this region (Fig. 22–12A). These rather strange forms represent the only regions of space that produce fused visual images of point sources of light under the selected conditions of fixation. Linksz (16) has suggested that the fusion horopter has the form of a torus, but his analysis is based on an incorrect assumption and is not empirically validated, as has been pointed out in a previous section.

## Spatial Limits of Fusion

It is common clinical experience that larger objects in the field remain fused over a greater range of distances than smaller objects. It is also evident that blurred images will show a greater fusional range than sharply focused images. To this extent, fusion depends on the spatial extent of the stimulus.

More systematically, Tyler has examined fusion as a function of size of the waves in a sinusoidal line stimulus (37). A sinusoidal wavy line was presented to one eye to be fused with a straight line in the other. When the stimuli were horizontal, the threshold for fusion remained reasonably constant (Fig. 22–13), but when the stimulus lines were vertical, Panum's area varied dramatically with the size of the waves (or spatial frequency$^{-1}$). The maximum retinal disparity could be as much as 1° when the waves had a period of 30° per cycle, and became as small as 2′ when the period was reduced to 20′ per cycle. This all occurred with the stimulus passing through the fovea.

Thus, the traditional concept of Panum's

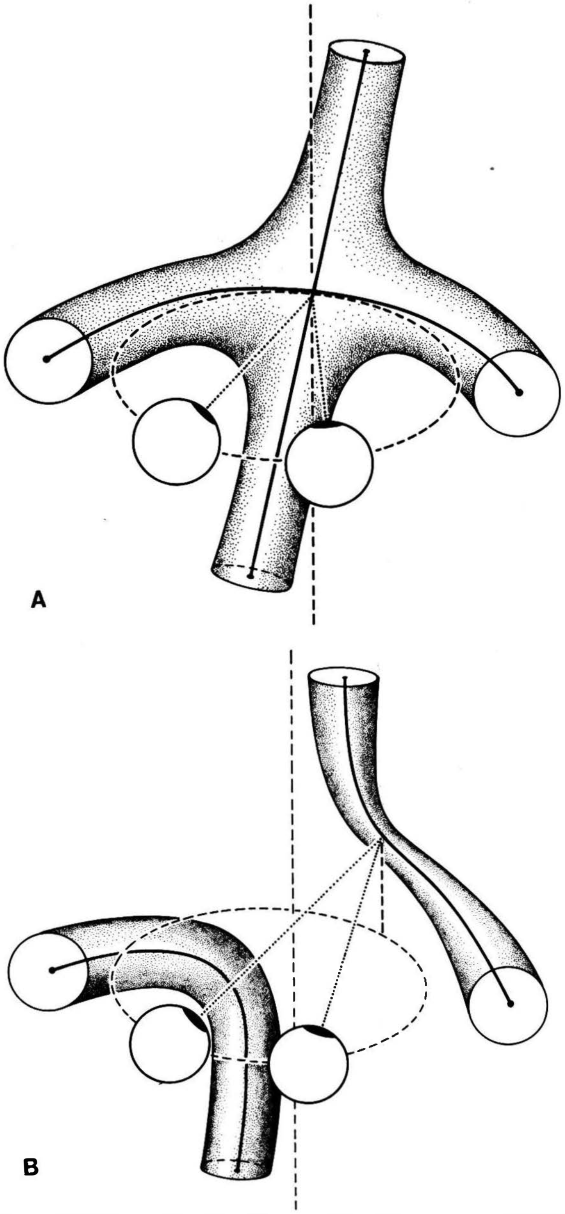


FIG. 22–12. A. The empirical fusion horopter for symmetric fixation in the visual plane. Note the spread away from the geometric horopter (dashed line) due to the Hering-Hillebrand deviation, and the vertical tilt due to the Volkmann-Helmholtz shear of the vertical meridians. B. The generalized empirical fusion horopter for any other fixation point. Note that asymmetric fixation produces a dramatic reduction of the fused region near the fixation point.

area as a fixed property or a given retinal region must be abandoned. Instead, the fusional extent is strongly dependent on the stimulus used to measure it. Hence, the fusional horopter presented in the previous section is not a fixed range around the point horopter, and the depictions of Figure 22–12 must be taken only as an indication of the fusional range in the real world, which will expand and contract according to the objects present in the field and the optical characteristics of the eyes viewing them.

## Temporal Aspects of Fusions

One interesting aspect of the fusion limit is that it is established in a very short time. Helmholtz (13) had experimented with fusion in stereograms illuminated by a (microsecond) electric spark. Woo (38) examined the effect of duration systematically and found that fusion appeared to be complete by about 30 msec. This is probably the same as the luminance integration time under his conditions, so the speed of simple fusion seems to be limited mainly by the rate of integration of luminance.

On the other hand, the fusion of complex targets is a very different matter. It is possible to generate fields of dynamically changing random dots which are identical in the two eyes (and can be perceived as fused) or entirely complemented in contrast in the two eyes (and essentially perceived as unfused). Fusion will persist even though the dots are rapidly changing, providing they always occupy corresponding positions in the two eyes. Such a stimulus provides the opportunity to examine the speed of fusion and defusion in complex stimuli. A change from correlation (correspondence) to complementation between the eyes is not visible to either eye alone when the random dots are dynamically changing.

Julesz and Tyler (39) used this paradigm to show that the minimum time required for fusion between two periods of unfused stimuli (complemented fields) was an average of 30 msec. But when they studied the time required to detect a break in fusion immediately followed by a return to the fused stimulus (identical fields), the time required was dramatically shorter, an average of 4 msec. This kind of temporal anisotropy was found to be a particular property of the fusion mechanism and no equivalent effect occurred for a comparable stereoscopic task.

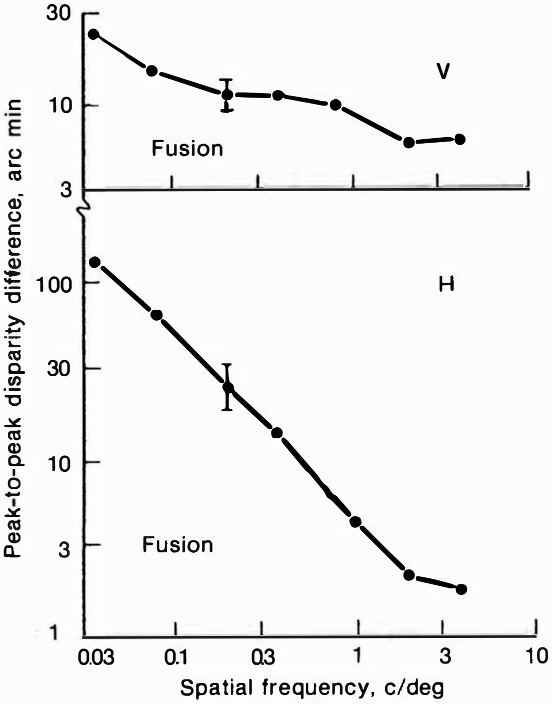


FIG. 22–13. Fusion limit as a function of stimulus pattern. For horizontal (**H**) disparity, fusion limit increases for stimuli with large cycles and decreases for stimuli with very small cycles. For vertical (**V**) disparities, the fusion limit remains much more constant. (Tyler CW: Vision Res 15:583–590, 1975)

## Evoked Potentials and Fusion

Many types of binocular interaction are reflected in the visual evoked potential (VEP) recorded from the human scalp. These fall into the categories of binocular summation, binocular rivalry and suppression, and stereopsis, each of which will be considered separately in the appropriate sections.

Evoked potential amplitude shows partial binocular summation under most conditions of binocular corresponding stimulation, whether the stimulus is a uniform or patterned flickering field (40–42) or an alternating pattern of some kind (43). Here complete summation is defined such that the binocular response is the algebraic sum of the two monocular responses, or the stimulus contrast required to produce a given response is half as great for binocular stimulation as compared with a monocular condition. In fact, most of the studies cited report partial binocular summation on the order of 1.4 greater than the mean monocular response, both for high-contrast stimulation and close to threshold response. However, these studies all involved transient evoked potentials measured at a single peak. An earlier study by Spekreijse (44) had utilized sinusoidal flicker of a uniform field for the stimulus. This revealed that in many circumstances high-amplitude stimulation produced saturation of the VEP, which could eliminate any appearance of binocular summation. Often an appropriate choice of contrast and field size would reveal full (2·0) summation.

More detailed work using sinusoidal patterns flickering in counter–phase at high rates (e.g. 30 reversals/sec) has shown that the degree of summation depends on the precise stimulus configurations and can vary from values of 1.0 to high values of 5.0, representing marked facilitation in the binocular response relative to the mean monocular response (44a), Binocular facilitation is presumed to reflect the activity of stereoscopic neurons, and is discussed in a later section.

## DICHOPTIC STIMULATION

When binocular stimuli fall on noncorresponding points on the two retinas, the stimulation is strictly described as dichoptic, or different in the two eyes. There are five classes of percept which are obtained, depending on the degree of noncorrespondence between the stimuli:

1. Depth with fusion
2. Depth with diplopia
3. Diplopia without depth
4. Binocular rivalry and suppression
5. Binocular luster

The first two classes are dealt with in the section on stereoscopic vision. They are not generally referred to as dichoptic, since the two retinal patterns are sufficiently similar as to be combined into a unified impression (particularly for fused stereopsis). The latter three classes are clearly dichoptic. There is not much to be said about diplopia, except as an indicator of the failure of fusion. As such, it has been included in the previous section. This section on dichoptic stimulation is therefore restricted to three topics, binocular rivalry, binocular suppression, and binocular luster.

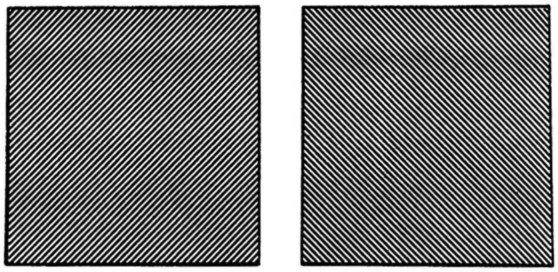


FIG. 22–14. Stimulus demonstrating strong binocular rivalry when left panel is viewed by left eye and right panel is viewed by right eye in the same retinal location.

### BINOCULAR RIVALRY

If the images in the two eyes are sufficiently different not to fuse and if they fall in the same general visual direction, the resulting conflict is resolved, not by binocular summation, but by a temporal alternation between one image and the other. In a given region of retina, the image in one eye predominates while the other is suppressed, and suddenly the suppressed image emerges into perception and dominates the region (see Fig. 22–14).

Binocular rivalry fluctuations are similar in many respects to fluctuations of attention, and are widely supposed to be under voluntary control. Actually, a number of studies have found that there is very little voluntary control over which eye dominates at any given time (45). The change of dominance is not affected by eye blinks (46) or by variations in accommodation or pupil size (47). In fact, the fluctuations in rivalry are well described by a sequentially independent random variable with no periodicities, as though the arrival of each change in dominance had no effect on the occurrence of subsequent changes (48).

A series of studies by Fox and his coworkers on the characteristics of binocular rivalry have made some headway in localizing the site in the visual pathway at which rivalry operates. Even though the localization is derived by inference from psychophysical evidence, it is quite significant in determining the processes of binocular cooperation and their breakdown in pathologic conditions. With the use of a monocular detection probe stimulus, Fox and Check (49) found that there is a real suppression of the incoming stimuli in the suppressed eye, rather than a relative facilitation in the salient eye.

The suppression has a number of interesting characteristics:

1. The suppression state is inhibitory. Test stimuli presented during suppression are attentuated relative to the same stimuli presented during dominance or during nonrivalry conditions. This is true for a variety of test probes and testing procedures, including forced-choice detection of incremental light flashes, forced-choice recognition of letter forms, and reaction time for detection of targets set into motion during suppression (49–53).
2. The magnitude of the inhibitory effect varies among subjects and with stimulus conditions, but is generally about a factor of 3, a value frequently observed in studies of saccadic suppression and visual masking.
3. The inhibitory effect of suppression endures throughout the duration of the suppression phase, and the magnitude of the inhibition remains constant (54).
4. The inhibitory suppression state acts nonselectively on all classes of test stimuli independent of their similarity to the rivalry stimulus. Evidence of nonselectivity is the attenuation of several different kinds of test probe stimuli. More systematic evidence of nonselectivity is provided by experiments that use a spatial frequency grating as a rivalry stimulus and then change either frequency or orientation of the grating during suppression while keeping mean luminance and contrast constant. Changes in orientation of 45° and of a factor of two or more in frequency remain undetected (55).

These studies suggest that rivalry is a process that is rather independent of monocular pattern recognition, but is triggered by a binocular mismatch, and then continues with its own characteristics independent of most stimulus parameters. However, one factor that is very important is the stimulus effectiveness in each eye. The higher the stimulus strength (in terms of luminance, contrast, or movement) in one eye, the greater the suppression of the other eye. If the stimulus strength is increased in both eyes equally, the rate of alternation between the two increases (48, 56–58).

Finally, two interesting experiments have explored the relationship between aftereffects of visual adaptation and rivalry suppression. For the motion aftereffect (59), threshold elevation, and spatial frequency shift after adaptation to a grating (60), perceptual occlusion of the stimulus during binocular rivalry did not affect the strength of the aftereffect, whereas equivalent physical occlusion of the stimulus reduced the aftereffect dramatically. In effect, the brain was adapting to an invisible stimulus. Since these aftereffects are almost certainly cortical, binocular rivalry must be occurring at a higher level in the cortex.

## EVOKED POTENTIALS AND BINOCULAR RIVALRY

Pattern reversal VEP can be recorded during binocular rivalry conditions. Cobb, Morton, and Ettlinger (61) used a stimulus with vertical bars to the left eye and horizontal bars to the right eye, with pattern reversals at 12 Hz, 180° out of phase for the two eyes. The response changes from the phase appropriate to each eye were well correlated with the subjective responses indicating changes in perceptual dominance at any given moment. No correlation was found between rivalry suppression and the amplitude of potentials evoked solely by luminance changes.

Similarly, Van der Tweel, Spekreijse and Regan (62) found that perceptual suppression of a flickering pattern presented to one eye by a static pattern presented to the other eye was accompanied by almost complete suppression of the VEP from the stimulated eye.

How do the VEP rivalry data accord with neurophysiology? The two are in conflict, for the known physiology would suggest that during rivalry the monocular neurons for both eyes would be stimulated, whereas the VEP reflects the subjective suppression of one eye at a time. It therefore appears that the site at which the pattern VEP is generated (at least for low frequencies of alternation) is beyond the level of binocular rivalry in the cortex. The rivalry process must then inhibit the response of one set of monocular neurons at a time, producing the reduction in the VEP.

## BINOCULAR LUSTER

Binocular luster is the final class of perception that can occur with noncorresponding stimuli.

It occurs in areas of uniform illumination in which the luminance or color is different for the two eyes. It was described by early authors in visual science, such as Panum (29) and Helmholtz (13), as a kind of lustrous or shimmering surface of indeterminate depth.

In fact, it may be said that the lustrous appearance of surfaces like a waxed tabletop or a car body is essentially due to binocular luster. It results from the different position of partially reflected objects in the surface by virtue of the different position of the two eyes. This kind of lustrous appearance is distinct from both the shininess of a surface as seen by reflected highlights and from the clear depth image seen in a mirror. The lustrous surface appears to have a translucent quality of depth due to diffusion from the surface, as well as the partial reflection providing a fixation plane at which the partially reflected image usually has a large disparity, and hence, areas of binocular luminance difference.

That the phenomenon of binocular luster has been largely ignored except as an incidental observation is surprising in view of the fact that it is qualitatively different from depth, diplopia, or rivalry. The lustrous region is not localizable in depth, but it seems unitary and does not fluctuate in the manner of binocular rivalry.

Recent work (39,63,64) has demonstrated that binocular luster may also be observed in static and dynamic random dot stereograms in which all the elements have opposite contrast in the two eyes. These studies have shown that detection of binocular luster is even more rapid than the detection of depth changes, and can be accomplished for a presentation of random dots of opposite contrast interocularly for only 2 msec with masking stimuli beforehand and afterward. This remarkable performance is the most powerful yet demonstrated for any exclusively binocular (cyclopean) task, and suggests that binocular luster is a phenomenon worth further study.

## STEREOSCOPIC VISION

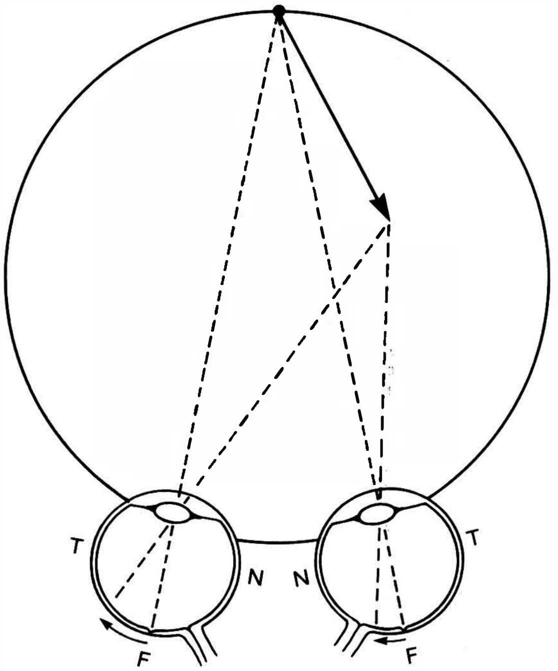
### BINOCULAR DISPARITY

Stereoscopic vision may be defined as the ability to see depth in the third dimension of visual space (specified in egocentric coordinates as distance from the observer) on the basis of relative binocular information on the two retinas. The fact that the two eyes are horizontally separated in space implies that they will in general receive slightly disparate views of all objects located nearer than infinity. The field of *horizontal binocular disparities,* combined with information as to the fixation directions of the two eyes (convergence), provides a precise, quantitative description of the distance of the objects in the field.

Considering the situation close to the line of sight for simplicity, if both eyes fixate a point object at a given distance (bifoveal fixation), the image of that object will obviously fall on the fovea in each eye. There will then be no binocular disparity between the two monocular images. If the point object is now moved closer to the observer, a difference in depth may be signaled in two ways, convergence and binocular disparity.

The image shifts in a temporal direction in each eye, producing a binocular disparity (Fig. 22–15). This can be interpreted neurally as a depth relative to the point of convergence. When the object is in front of the point of

FIG. 22–15. Horizontal binocular disparities arise from objects (e.g., **arrow**) at different distances, and give rise to stereoscopic depth perception. Here the arrowhead has a greater eccentricity on the temporal (**T**) retina of the left eye than on the nasal (**N**) retina of the right eye. Fixation is with the fovea (**F**).



convergence, the lines of sight of the monocular images cross before the convergence distance, giving rise to a crossed disparity. If, on the other hand, the object were moved away from the observer, it would be behind the convergence point. The lines of sight would not cross before the convergence distance, and the disparity would be described as uncrossed.

Note that it is a mistake to regard the nasal or temporal retina as being associated with specific depth information, as has sometimes occurred. A nasal shift in crossed disparity and temporal shift for uncrossed disparity does not mean that the images fall on the nasal and the temporal retina, respectively, unless the images are at or close to the fovea. Thus, if the near object is viewed at 5° eccentricity to the left, the images will always fall on the temporal retina in the left eye and the nasal retina in the right eye for all disparities (up to 5°), whether crossed, zero, or uncrossed.

A second result of moving the object closer is that the eyes may converge to the new vergence angle so as to reacquire bifoveal fixation. The difference in vergence angle provides the cue to the new distance of the object, since the binocular disparity is again zero. Thus vergence angle is a cue to depth which is distinct from, and interacts with, retinal disparity.

## PSYCHOPHYSICAL STUDIES

### Precision of Stereoscopic Localization

Under normal conditions, most observers with no ocular abnormalities can discriminate a depth difference between two images with a relative disparity of only about 10 arc sec (0.0028°). The best values reported in the literature are obtained using a method of constant stimuli, in which the observer is presented with a series of disparities between a test and comparison rod stimuli and asked to discriminate whether the test rod is nearer or farther than the comparison rods (64). Whether monocular information is present or is eliminated (65), the best observers achieve a 75% discrimination level close to 2 arc sec (0.00056°).

This appears to be one of the finest spatial discriminations of which the human visual system is capable, and it represents a truly amazing accomplishment, particularly considering that the resolution limit for dark lines is more than 10 times larger at the intensities used in the stereoscopic discrimination tasks (66) and also that the discrimination necessitates comparing between two retinas in continuous motion due to eye movements. To illustrate the refinement of this discrimination, it can be converted into real distances for the near and far limits of vision. For the closest fixation of 10 in. away, the best stereoscopic threshold corresponds to the appreciation of a depth of one-thousandth of an inch (25 $\mu$). For comparison, this is finer than the size of a typical human ovum (100 $\mu$) or the cell body of a typical neuron (50 $\mu$). Conversely, when looking at the horizon, one has stereoscopic discrimination that objects 2 miles away are nearer than the horizon. This allows, for example, stereoscopic discrimination of depth in some types of clouds. These limits provide useful stereopsis over an extensive range of environmental conditions.

### Spatial Limits of Stereopsis

Although stereoacuity is excellent at the fovea, this threshold rises with an accelerating function as the stimulus is moved into the periphery (67), so that stereopsis rapidly becomes very poor beyond about 20° eccentricity, or outside the circle passing through the two blind spots in the binocular visual fields.

Just as a binocular disparity can be too small to elicit a perception of depth, disparity can be increased until it is too large for depth perception. As pointed out before, depth continues to be present well beyond the range of binocular fusion. The upper and lower disparity limits for depth and the intermediate limit for fusion are shown as a function of eccentricity in Figure 22–13. This graph makes the important point that there is as large a region of stereopsis for which the stimuli are diplopic as there is when they are fused. In fact, the greatest perceived depth is found beyond the region of fusion.

Ogle (24) refers to these regions as quantitative (for fused) and qualitative (for diplopic) stereopsis, but his terms are inaccurate, because the perceived depth may be quantified in both regions, as has been shown by Richards and Kaye (68) (see Fig. 22–16). It therefore seems more appropriate to designate the two regions as fused and diplopic stereopsis, thereby avoiding pejorative implications.

Another property which is roughly related to these two regions is that perceived depth increases linearly with binocular disparity in most of the fused region, whereas it falls with some nonlinear function through the diplopic region. However, the transition from a linear to nonlinear function does not occur at exactly the same disparity as the transition from fusion to diplopia, so the correspondence between the two divisions is not precise.

Richards and Kaye (68) further measured the depth magnitude function for different widths of the test bar. The maximum depth occurs at disparities varying from 0.5° to about 2°, and a disparity that can produce no depth impression at all for a small stimulus (say, 1°) may be optimal for depth perception in larger test objects. This suggests that tests for stereoscopic vision should involve stimuli with a good range of sizes and disparities in order to be sure of the capabilities of an abnormal visual system.

Another way of demonstrating the effect of stimulus size on stereoscopic ability was described by Tyler (37). A straight vertical line was presented to one eye and a line consisting of vertical segments displaced alternately to the left and right to the other eye. Upon fusion, the segments are seen alternately forward and back from the fixation distance. The maximum disparities for which depth was perceived were inversely proportional to vertical length of the segments over a range from 0.05°–5°. This was termed **disparity scaling of the upper depth limit.** Such disparity scaling reduces the complexity in processing the three-dimensional image, while retaining the full range of sensitivity to disparities from degrees to seconds. Thus it is possible to appreciate many aspects of a three-dimensional scene without requiring an order of magnitude of more neurons than are needed for a two-dimensional scene.

A similar limitation occurs in the lower limit of stereopsis, stereoacuity. Mitchell and O'Hagan (69) have shown that the clear vertical distance flanking a stereoscopic test object is important in stereoacuity. The threshold was markedly degraded when monocular flanking lines were present closer than about 20′ above and below the disparate objects. Similarly, Tyler (36), using a sinusoidal wavy line version of the alternating stereoscopic segment stimulus, found a progressive degradation as the adjacent segments were brought closer than 20′. Although the stereoscopic system can process extremely fine disparities, there is a much coarser resolution for spatial changes in disparity, as if the system needs a reasonable size of stimulus on which to perform the disparity computation.

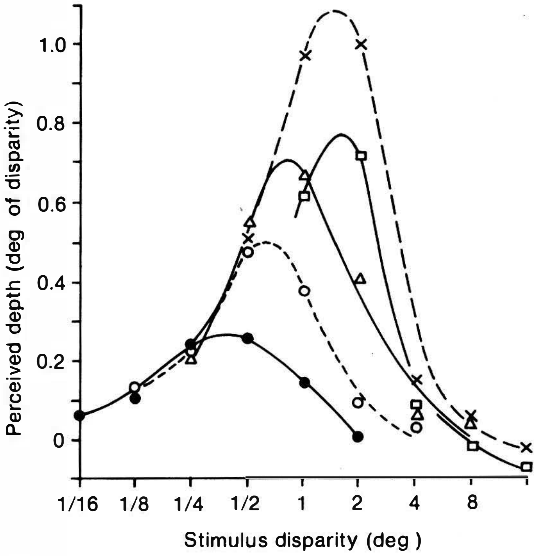


FIG. 22–16. Relative perceived depth vs. stimulus disparity averaged for three observers. Crossed (convergent) disparities only. Each curve represents a separate bar width: **dots**, 0.5°; **open circles**, 0.1°; **triangle**, 0.2°; **cross**, 0.4°; **square**, 0.8°. Bar height was fixed at 0.5°. (Richards W, Kaye MG: Vision Res 12:437–454, 1972)

## CYCLOPEAN STEREOPSIS

An important advance in terms of both experimental analysis and controlled clinical testing of stereopsis was the development of random-dot stereograms by Julesz (39). The basic idea is to present to each eye with a field of random dots containing a camouflaged stereoscopic figure. An early version of this approach was conceived by Ames in the form of a "leaf room" (24). All sides of the room were covered with leaves to obscure the monocular perspective information of its shape. The room appeared almost flat when viewed with one eye, but appeared to spring into vivid depth on opening the other eye. The shape of the room was predictably altered by placing different types of magnifying lenses before one eye.

Julesz (39) demonstrated with computer-generated random-dot patterns that it is logically possible to produce a complete dissociation between the monocular and binocular patterns. If the dot pattern in one eye is completely random, then elements may be shifted and rearranged, but the result is another random pattern with no hint of the rearrangement that has occurred. If two such patterns are presented dichoptically, the visual system may utilize the correlation between the two to perceive the relative pattern shifts. If the shifts are horizontal, they constitute a binocular disparity and give rise to a stereoscopic depth figure which is literally invisible with either eye alone. (Other types of shift give rise to various types of binocular rivalry and luster percepts.)

An example of a random-dot stereogram with a square stereofigure is shown in Figure 22–17, which may be viewed in a stereoscope or by free fusion of the image (crossing the eyes so as to produce three perceived random-dot fields, the central one binocular and the other two monocular).

The importance of random-dot stereograms is that they demonstrate that a monocular form is not necessary for the perception of a stereoscopic form. The stereoscopic form is first present at a binocular level in the cortex that Julesz designated as **cyclopean.** (This term should be distinguished from the cyclopian eye of Hering, which refers to the position in the head from which binocular visual direction is perceived.) The cyclopean level of neural processing then provides a bench mark to determine the relative locus of different functions. For example, Julesz (70) has found that a large number of visual illusions persist when presented so as to be visible only at the cyclopean level. The residual illusion must, therefore, be located in the cortex, rather than in the eye.

Clinically, random-dot tests of stereovision are important, as it is impossible to fake the response by looking first with one eye and then the other, since neither contains the stereoscopic figure. However, perception of the form may be possible by binocular luster alone, so that to demonstrate stereopsis unambiguously, it is necessary to test for the direction of depth perception towards or away from the observer.

## PHYSIOLOGICAL STUDIES

### Physiologic Basis of Stereopsis by Spatial Disparity

The first requirement for neural processing of the stereoscopic depth information available on the two retinas is some means of comparison of similar stimuli and their minute positional differences on one retina relative to the other. In the visual cortex the comparison can be made by neurons with receptive fields in the two eyes. Accordingly, the first attempt at an explanation of the physiologic basis of stereopsis was in terms of disparities between the positions of the receptive field in each eye for binocular neurons (8,34). This now seems more likely to be the basis for binocular fusion only, since the minimum size of receptive fields in monkey cortex (33) seems to be about 15′, which would give a range of disparities of about half a degree—a far cry from the disparities of a few arc seconds which can be discriminated behaviorally.

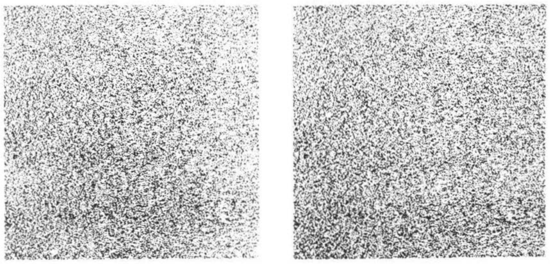


FIG. 22–17. Random dot stereogram. When the left and right images are fused stereoscopically, a spiral in depth will appear. These arrays are arranged so that the reader may free-fuse by crossing the eyes to see the spiral pointing upward. (Julesz B: Foundations of Cyclopean Perception. Chicago, University of Chicago Press, 1971)

A much more sensitive mechanism of tuning cells for binocular disparity is revealed by looking at binocular interactions with simultaneous stimulation of the two retinal receptive fields (32,71,72). Many cells show facilitative and inhibitory interactions as binocular disparity is varied within the range of the receptive fields (defined by stimulation of each eye separately). Thus, the region of binocular facilitation over the monocular response may be an order of magnitude narrower than the size of the receptive fields. Furthermore, stimulation of flanking regions often shows binocular inhibition of the response, providing further tuning of the disparity range of the cell. Such binocular interactions may well be the first stage of the mechanism by which the cortex processes the hairsbreadth disparities present between the binocular retinal images (72).

## Other Types of Disparity Tuning

The spatial disparity tuning of cortical neurons is not restricted to neurons with a region of binocular facilitation. Recently, Poggio and and Fischer (73) suggested a classification of binocular interactions of neurons in the cortex of the behaving monkey into four classes, illustrated in Figure 22–18. Neurons that are predominantly binocular (in the classical sense of having identifiable receptive fields with monocular stimulation of each eye) tend to show either binocular facilitation (a) or a region of binocular occlusion (b). More surprisingly, they found that cells with classically monocular receptive fields showed binocular facilitation for either crossed (c) or uncrossed (d) disparities only. This is exciting, as it suggests a neural basis for fine (fused) stereopsis and coarse (diplopic) stereopsis.

Blakemore, Fiorentini, and Maffei (74) have pointed out that, in addition to a spatial binocular disparity, the fact that cortical cells have oriented receptive fields implies that there may also be orientation disparities between the receptive fields of the two eyes. They found that such orientation disparities were present in cat neurons, and hypothesized that they might be involved in the processing of vertical tilt in depth. Detection of a depth tilt in this manner has the advantage that the orientation cues are independent of the distance (hence, spatial disparity) of the object (75).

Finally, Pettigrew (76) has reported cells with opposite preferred directions in the two eyes. Such cells would be well suited to detect motion in depth toward or away from the observer. Cynader and Regan (77) have shown that many cells, particularly those showing binocular occlusion, have a binocular interaction specific for motion in depth, *i.e.,* motion in opposite directions on the two retinas.

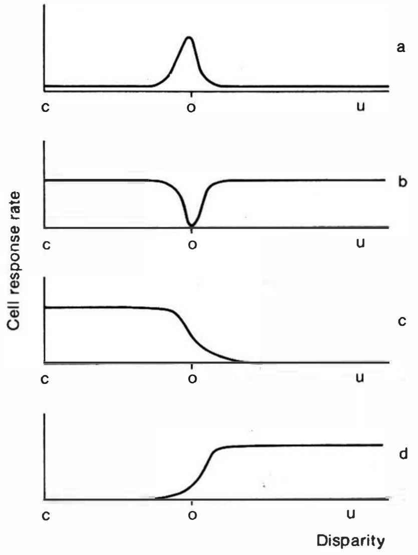


FIG. 22–18. Four classes of binocular disparity sensitivity in monkey cortex from crossed (**c**) through zero (o) to uncrossed (**u**) disparities; (a) binocular facilitation; (**b**) binocular occlusion; (c) monocular, crossed; and (**d**) monocular, uncrossed sensitivities. (Poggio CF, Fisher B: J Neurophysiol 40:1392–1405, 1977)

## Evoked Potentials and Stereopsis

From the point of view of objective evaluation of stereopsis in young strabismus patients, it would be of value to be able to measure scalp potentials evoked solely by stereoscopic stimuli. There have been three recent techniques reported by which a stereoscopic VEP can be isolated. The first method is to determine binocular facilitation in the pattern VEP. The second is to present a disparity shift in a static random-dot stereogram. Only the third method, a disparity shift in dynamic random stereograms, eliminates all monocular contamination of the VEP. However, it is too early to say whether any of the methods provide unequivocal evidence of stereopsis, as will be explained.

A form of binocular facilitation linked to stereopsis was first reported in a brief study by Fiorentini and Maffei (78). They found a case in which the VEP amplitude to an alternating grating stimulus increased when the grating had a slightly different frequency in the two eyes, and hence appeared tilted in depth. However, it was not established for what range of conditions or what proportion of the population this effect would be obtained. Srebro (79) found that some binocular facilitation, in the form of a binocular response greater than the sum of the two monocular responses, occurred in about 70% of a normal group. This facilitation was not seen in three patients with small angle esotropia. However, binocular facilitation in esotropia is reported by other authors (80).

Binocular facilitation in the VEP could, in general, be a property of either the binocular fusion system or the stereoscopic system. However, if the stimulus is a horizontal grating, it can contain no horizontal disparity information. Apkarian, Nakayama and Tyler (81) showed that when marked binocular facilitation was obtained for VEP responses to vertical alternating grating stimuli, rotating the grating to horizontal reduced the response to about the sum of the monocular responses. If rivalry was induced by presenting a vertical grating to one eye and a horizontal to the other, the response fell almost to the level of a single monocular response. These results support the idea that summation is a property of the binocular fusion system and facilitation of the stereoscopic system.

A more direct approach to the stereoscopic VEP was taken by Regan and Spekreijse (82), using static random-dot stereograms (see Figure 22–17). The VEP was recorded in synchrony with a change in disparity of the center region of the stereogram. These investigators found a large response when the disparity change was in the vertical direction, and approximately double the response when the disparity change was horizontal. Presumably, the vertical disparity response represented the activity of the fusion system, and the increase in horizontal disparity response was due to inclusion of the stereoscopic system. But since the change in disparity was produced by a monocular shift of the dots in one eye, the role of the monocular response in the binocular facilitation could be isolated.

The solution to the problem of the monocular response lies in presenting the disparity in a field of dynamic random-dots, continually changing position at random. Now the change in disparity is completely hidden in the stream of monocular changes, so that there is no monocular event to trigger a response. The VEP is therefore purely cyclopean, and a large response can be obtained (83). However, there is still an ambiguity as to whether the response originates from the fusion or the stereoscopic system.

## DEVELOPMENT OF BINOCULAR VISION

### NEUROPHYSIOLOGY OF DEVELOPMENT

At birth, the retina and optic pathway are not completely developed, although the basic receptive field organization of neurons and cortical architecture are present (84). Neurophysiologic studies have demonstrated that the properties of neurons in the visual cortex are markedly influenced by visual experience during the first few postnatal months. Specifically, these neural properties have been determined to involve a) binocularity, b) orientation specificity, and c) disparity specificity. The excitatory connections of receptive fields located in both retinas or retinotopic projections (85,86) are largely present at birth. However, simultaneous occurance of patterned visual input to both eyes during the developmental period is necessary to maintain their association (87).

There is a great degree of plasticity in the neonatal visual system of the cat (88–91). Patterned visual stimuli seem to act not only as a catalyst but also as directional stimuli in the consolidation, maintenance, and refinement of the neuronal connections in the visual cortex. Any disruption to the normal developmental conditions, such as a congenital or early-onset ocular misalignment or significantly subnormal vision in one eye, can prevent the eyes from developing the normal functional interrelationship.

A possible function of this plasticity in neuronal properties during early visual experience would be to allow the opportunity to match the properties of feature-detecting cells to the commonest features in the animal's visual world, maximizing its capacity for analysis of the more important components of its environment (92,93). Also, the capacity to make modifications in optimal disparity and preferred orientation would ensure that binocular cortical cells adopt similar receptive field positions and preferred orientations on the two retinas. This establishment of precise disparity selectivity and similar preferred orientation in the two eyes is a primary requirement for the probable role of these cells in binocular fusion and stereopsis, as hypothesized in previous sections. This would account for the loss of binocularity with a large angle of strabismus, since the retinal images would be misaligned beyond the range of compensation of receptive field disparity.

In both immature visual systems and binocularly deprived visual systems, the binocular responses of cortical neurons are observed to tolerate a wide range of retinal disparity, while visual experience narrows this range. Thus, early plasticity seems to be vital to the formation of cells with closely matched recep-

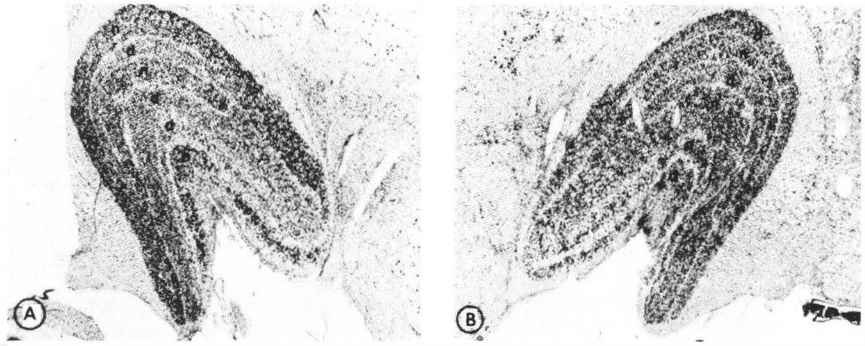


FIG. 22–19. Right (**A**) and left (**B**) LGN of a monkey reared with monocular lid closure. Note poor staining characteristics in all layers receiving input from the deprived eye (**d**) compared with those receiving input from the normal eye (**n**), particularly in the two ventral layers, which contain predominantly Y-cells.

tive field properties in the two eyes, which is a necessary condition to form the substrate for stereoscopic vision. Blakemore and Van Sluyters propose that "genetically specified, predominantly monocular, simple neurons initially provide a 'conditioning' input to future complex cells and entrain them to respond to the same orientation. Both cell types ultimately gain matched input from the two eyes" (86).

There are well-established postnatal morphologic changes in the retina and retinal projections relative to the presence or absence of visual stimuli. In the lateral geniculate nucleus (LGN), neuronal cell growth is greatly reduced (by 25%–40%) in the laminae with connections to visually deprived eye as compared with a nondeprived eye (87,94) (Fig. 22–19). In studies where one eye had been deprived since birth for three months and was then allowed visual stimuli and the other eye then deprived, the difference in cell size between the LGN laminae was decreased and even reversed (95).

The two types of retinal ganglion cells and geniculate cells (96) seem to be differentially affected by such deprivation (97). The large cells of the binocular segment (which are found mainly in the peripheral field projections) are much more affected than either the large cells of the monocular segment or the small cells found mainly in the projection of the area centralis.

In the cat there is also a pronounced difference between the visual field defects, depending on whether there has been monocular or binocular deprivation. Following monocular deprivation, there is a reduction in growth among the large cells of the binocular segment, but not in the monocular segment. With binocular deprivation, there is overall cell shrinkage in both segments, but to a lesser extent.

In the adult cat most of the cells of the superior colliculus of the midbrain are binocularly driven. Visual deprivation in kittens has consequences in the superior colliculus that can be considered to reflect changes in the visual cortex and, hence, in the corticotectal projection which is presumed to provide binocularity. The results of monocular deprivation experiments seem to suggest that there is functional competition for effective synaptic input dependent on the actual firing pattern of afferent synaptic fibers, and that this represents a crucial process underlying the course and nature of the development of the visual system (91). The dependence on visual experience during maturation appears to involve its crucial role in refining these functional processes; however, its deprivation does not prevent these processes.

The physiologic deficits observed in animals suggest a basis for understanding various human perceptual disorders. Monocularly deprived kittens fail to develop the normal proportion of binocularly driven cortical neurons if this monocular deprivation is imposed during a specific stage in their maturation, which has been determined to be 4 through 12 weeks (98,99). Also, misalignment of the visual axes (which results in discordant binocular input) interferes with the development of binocular neurons when experimentally induced during this same period

(91,100). Subsequently, it was determined that orientation specificity (89,90,101) and disparity specificity (102,103) of cortical neurons (in the cat) are similarly dependent on visual experience in that early postnatal period.

## ABNORMAL DEVELOPMENT OF BINOCULARITY IN HUMANS

**Strabismic amblyopia.** Amblyopia occurs in two major forms. The first is strabismic amblyopia. Functional competition between the two eyes seems to be a major factor in this condition. If each eye is used a portion of the time, no amblyopia develops. However, even though the retinal images may be clear in each eye, one eye may be used for fixation more than the other (for example, because it has better motor performance). Differences between the eyes will also lead to a preference for one eye, and the eye not used for fixation develops amblyopia. These differences could be in image focus (anisometropia), image magnification (aniseikonia), or partial occlusion of the image in one eye. Finally, profound deprivation amblyopia in one eye may lead to strabismus of that eye. Thus, all mixtures of deprivation and strabismic amblyopia occur.

Amblyopia in strabismus is more often associated with eccentricity of fixation than in mild deprivation amblyopia. In about 50% of comitant esotropia cases, the position of the retina used for monocular fixation by the amblyopic eye corresponds with its angle of strabismus (114).

Strabismic amblyopia is frequently seen in infants 4 or 5 months of age; such an esotropic eye may not even be able to fix a target. This suggests that the "sensitive period" for strabismic amblyopia has its beginning prior to this time. Amblyopia from a strabismus beginning after the age of 5 or 6 years is rare. Thus, the sensitive period for occurrence of strabismic amblyopia would seem to end at a time earlier than that for deprivation amblyopia.

The appreciation of stereopsis involves the analysis of spatially disparate retinal signals from each eye under the condition of binocular single vision. However, there are perhaps 4% of the population who seem to be unable to use these disparity cues and possibly another 10% who have difficulty in judging the type of disparity (*i.e.,* near or far) that they perceive (113).

One approach to the study of the presence and relative proportion of binocular cortical neurons in humans has involved the interocular transfer of orientation-specific aftereffects. That is, following adaptation involving only one eye, the amount of transfer of aftereffect to the unadapted eye (relative to the aftereffect observed for the adapted eye) is used as the measure of interocular transfer. If this interocular transfer is mediated by binocularly innervated cortical neurons, then the extent of the transfer should be an index of the proportion of cortical cells that are binocular.

Some recent reports involving both the tilt and motion aftereffects have noted a high correlation between the amount of interocular transfer from the adapted to the nonadapted eye and the level of stereoacuity. Among the individuals tested in both types of studies were stereoblind subjects who exhibited little or no interocular transfer as well as individuals with a range of levels of stereoacuity from poor to normal. The magnitude of the correlations was 0.86 for tilt aftereffect (96) and 0.75 for motion aftereffect (105). The demonstration of this association suggests that both stereopsis and interocular transfer seem to depend on the presence of binocular neurons.

The absence of binocular cortical neurons could be the result of an early impediment to normal binocular vision resulting in their functional loss, comparable with that demonstrated in kittens, or alternatively it could be the result of a congenital deficiency. Congenital anomalies of visual cortex are in fact known to occur in some animals, such as the Siamese cat (106,107). Other studies have shown that a childhood history of strabismus does not preclude the ability to exhibit interocular transfer (108,109). Two studies involving individuals with an early history of strabismus have utilized the interocular transfer phenomena to delineate the sensitive period in humans for the development of binocularity. Hohmann and Creutzfeldt (109) (Fig. 22–20) investigated the association between the levels of interocular transfer and the age at onset of the deviation and concluded that the end of the human critical period was approximately at 2–2.6 years of age. Additional support for this delineation of a critical period in humans for the development of binocularity is supplied by Banks, Aslin, and Letson (110), who propose that the critical period begins several months after birth and extends to approximately 1–3 years of age. Comparison of functional results from surgical correction of early-onset esotropia with age at correction provides additional weight to this argument. A summary of results (111,112) shows that no patients surgically corrected after the age of 2 years exhibited stereopsis, whereas more than 60% of those who were corrected before the age of 2 years have demonstrable stereopsis.

It has been suggested both directly and indirectly in this discussion that the presence and level of stereoacuity may depend on certain innate factors beyond those measured by the amount of interocular transfer that can be exhibited and the presumed proportion of binocularly driven cortical neurons.

**Deprivation amblyopia.** The second major category is deprivation amblyopia, which occurs when the image in one eye or both eyes is not normally clear. This may be from refractive error (astigmatism, aphakia), from interferences with clear optics (corneal scar, cataract), or from glare degrading the retinal image (albinism). The visual consequence depends on severity of deprivation, difference of deprivation between the two eyes, age at onset, and duration before treatment.

Profound defects in retinal imagery from birth (for example, dense cataract) affect the visual system so strongly that removal of the cataract after two years of age, even given a clear image and occlusion treatment of the good eye (if unilateral), is insufficient to restore useful vision above 20/200 (115).

Blur, if not too severe, may leave the visual acuity open to marked improvement through optical correction, even though the eye was deprived of clear vision during much of the development period. As an example, bilateral hyperopia of +8.00 diopters (present since infancy) when first corrected by glasses at age 5 or 6 typically gives a best corrected vision of 20/100. However, development of the vision over 2–3 years with corrective glasses results in a visual acuity of *almost* 20/20. Persistence of some amblyopia in such bilateral cases is also seen in amblyopia for the more hyperopic meridian in hyperopic astigmatism (115).

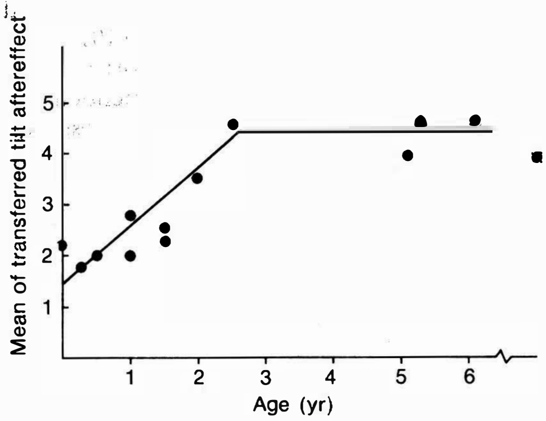


FIG. 22–20. Interocular transfer of aftereffect as a function of age of onset of strabismus. (Hohmann A, Creutzfeldt OD: Nature 254: 613–614, 1975)

Besides the severity, the *difference* in image clarity of the two eyes establishes the profoundness of amblyopia. It is a common clinical event to see cataracts develop or progress at age 3 or 4 years resulting in vision of 20/200 or less. When equal in both eyes, amblyopia does not usually occur, and 20/20 vision is often restored by surgery. Contrariwise, a unilateral cataract of such severity at such an age is a visual disaster unless rapidly treated (116).

If sufficiently severe, a deprivation in infancy cannot be reversed even after a few months of age. While this susceptibility progressively diminishes, untreated traumatic cataracts without other injury to the eye, acquired even after the age of 8, can still result in permanent amblyopia. However, after about the age of 10, amblyopia can no longer be produced even by the "total occlusion" of a cataract. The period of amblyopia sensitivity is over (117).

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