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Binocular Vision

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Eyes come in pairs, providing special capabilities that are not available to a single imaging system. This chapter provides an overview of the ways that visual processing has evolved to utilize the joint capabilities of a dual optical system for the perception of the third spatial dimension, of the visual deficits that can occur specific to the binocular coupling of this system, and of current approaches to ameliorating those deficits.

PHYLOGENETIC BACKGROUND

It is remarkable that virtually all animals have their eyes arranged in pairs, despite the tremendous variety in general morphology across species.¹ Cyclops are essentially unknown outside mythology. Over many types of image-forming structures, from the pigmented eyespots of the flatworm, the pinhole eyes of the nautilus, and the compound eyes of insects, to the familiar mammalian arrangement, all seem to favor a paired organization. Even among invertebrates, 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 may be suggested.

1. 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.
2. Two eyes may be used to achieve a 360-degree field of view, because optics are limited to approximately 180 degrees (in contrast to the compound eyes of insects, which have no inherent limit, but nevertheless always occur in pairs).
3. 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.
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. And, probably the most dramatic reason for binocular vision, two eyes permit stereoscopic depth perception—the ability to use the differences in the images caused by each eye viewing from a slightly different viewpoint, known as 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-degree field of view by having the eyes pointing in opposite directions. This advantage applies to fish, many birds, and to a large extent, mammals that are preyed upon. However, most predatory animals, from spiders and crustaceans through birds to mammals and humans, tend to have the eyes facing in the same direction. This arrangement is, presumably, to take advantage of stereoscopic depth perception, which has been demonstrated in humans, monkeys, cats, and falcons, and is likely to be widespread across other species.^{2–5}

Actually, almost all animals show some degree of binocular overlap, even those with a full 360-degree field.¹ The binocular overlap is almost exclusively in the forward direction (although it may be oriented upward or downward in different species). It is unclear, however, 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 (Fig. 1). They, therefore, have sufficiently good visual acuity to use binocular disparity cues for stereoscopic depth perception.

The relative unimportance of convergence angle as a primary cue to distance may be suspected by noting that many species have little or no convergence capability. This observation is true for many birds and, in particular, the owl, with its large binocular fields.⁶ A similar situation occurs in lemurs and would imply that convergence works mainly to optimize the alignment of the retinas for the assessment of binocular disparities for stereopsis rather than as a primary cue to distance. Still, some animals may use the muscular convergence information that allows minimization of disparity by aligning the eyes to help determine the distance of an object.

In addition to the benefits of binocular vision, any animal with two eyes obtains the advantage of duplication against dysfunction; if duplication were a principal advantage, however, a further proliferation of the number of eyes might be expected.¹ The advantage obtained

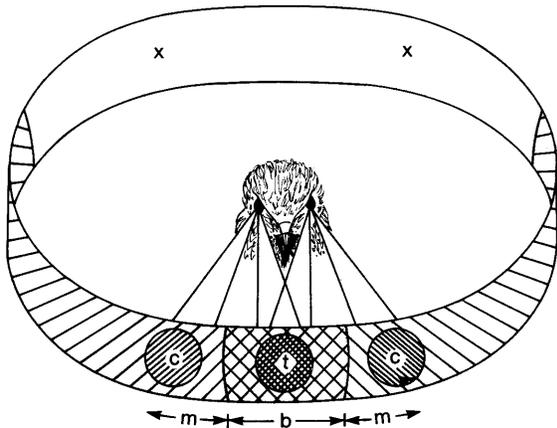


Fig. 1. Projection of the three regions of high acuity in the visual field of a hawk. The central foveae in the two eyes project to two monocular regions (c), while the temporal foveae in each eye project to a binocular region (t). In the case of this species, a rear portion of the field is out of view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

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.

SENSORY ASPECTS OF BINOCULAR VISION

With the two eyes aligned on a stimulus field, there are several sensory aspects of binocular vision that arise from the relative configurations of the stimulus details. These will be discussed on the assumption that the eyes stay aligned on a defined fixation target. Specifically, the alignment is defined by the angular direction of the region of highest acuity, the *fovea*. The orientation of the globe is referenced to this control region of the retina, centered at the back of the eye; angular distance from the fovea in any direction is known as *eccentricity* for targets in the visual field. In practice, of course, the eyes normally move to a variety of fixation positions both laterally and in depth as the observer moves the fovea to inspect a visual scene. However, the sensory processes need to be understood in terms of the effects of stable binocular presentation before the dynamic effects of moving eyes can be taken into account.

VISUAL DIRECTION

With the foveal fixation on one point, all other points in the visual field of one eye are seen as having different

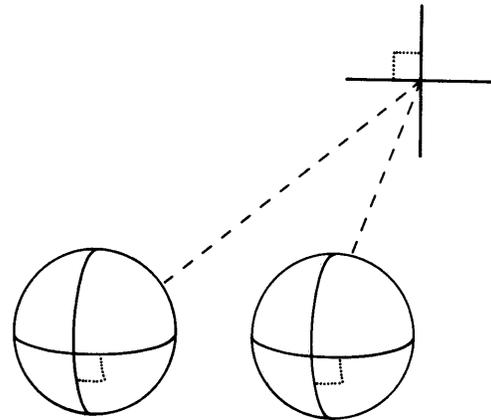


Fig. 2. Geometric retinal correspondence. When the eyes are aligned and viewing at infinity (*shown here in perspective*), a point at a given distance vertically and horizontally away from the fixation point (*dashed lines*) projects equivalent distances horizontally and vertically away from the foveae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

visual directions with respect to the fixation point. This two-dimensional spatial layout of visual directions is a defining property of the visual sense (as contrasted, for example, to the sense of smell, in which there is no spatial organization). If a stimulus point in space projects so as to have the same perceived visual direction in space when viewed with either eye, its image is considered to fall on retinal points that are exactly *corresponding* in the two eyes, as depicted in Figure 2. Departures from correspondence in the form of small differences between the image positions in the two eyes are termed *binocular disparities* (Fig. 3).

SENSORY FUSION

When there is a small binocular disparity in visual direction in one eye relative to the other, the binocular image still will be seen as a single fused image. The range of disparities for which *binocular fusion* occurs is known as *Panum's area*. When the images are fused, the two images combine into a joint percept that resembles the one seen by each eye alone. Beyond this region of fusion, images are seen doubled or in *diplopia*, such that the separate images for the two eyes are both perceived in their true monocular locations.

DICHOPTIC STIMULATION

Images that are very different at corresponding retinal locations in the two eyes (e.g., images that derive from the same stimulus but are shifted, rotated, or magnified so that dissimilar contours are present in corresponding

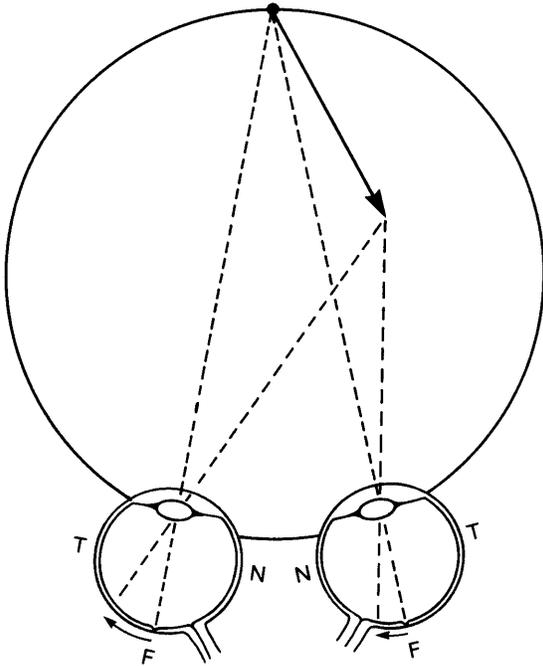


Fig. 3. Horizontal binocular disparities arise from objects (e.g., arrow) at different distances and give rise to stereoscopic depth perception. Here the arrowhead has a greater eccentricity on the temporal (T) retina of the left eye than on the nasal (N) retina of the right eye. Fixation is with the fovea (F).

locations) provide *dichoptic stimulation* conditions. If such dichoptic images are of high contrast, then a *binocular rivalry* will be set up between the two monocular images, so that the observer is aware alternately of the image to one eye and the image to the other. 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 because of *interocular suppression*.

If, however, the stimulus contrast is low for dichoptic stimuli, prolonged periods of *dichoptic summation* may be obtained, during which the different stimuli in the two eyes appear to be summed together as if their contrasts were added linearly throughout the dichoptic field. Dichoptic summation also is obtained for high contrast stimuli when the presentation time is brief (<150 msec).

STEREOPSIS

If two similar images are presented to the two eyes with a binocular disparity that has a horizontal component, the combined image will be seen in vivid depth nearer or farther than the point of fixation (Fig. 3) within some range of limiting conditions. *Stereoscopic depth* from

horizontal disparities is perceived both in the region of binocular fusion of the monocular targets into a single image and also in the region of diplopia, where the image appears doubled but clearly at a different depth from zero-disparity targets. *Stereoacuity* is the smallest disparity interval that produces reliable depth discrimination under particular conditions.

DEVELOPMENT OF BINOCULAR VISION

NEUROPHYSIOLOGY OF DEVELOPMENT

The fundamental anatomic basis for binocular vision in mammals is the partial decussation of the optic nerves of the two eyes to bring the retinal information from corresponding areas of each eye together at the cortex, as considered in more detail in Figure 15. From the point of view of a neuron in the cortex, the region of the retina in which it responds to changes in local illumination is called the *receptive field* of that neuron. Most neurons in the cortex have identifiable receptive fields in both eyes, either at corresponding locations or close to them. At birth, the retina and optic pathway are not completely developed; however, the basic receptive field organization of neurons and cortical architecture are present.⁷ 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 developing neural properties have been determined to involve:

Ocular dominance, the relative strength of response from a particular neuron for input from the two eyes

Orientation specificity, the degree of tuning of the response to one specific orientation of a line stimulus

Binocularity, the degree to which the binocular response exceeds the response to stimulation of each eye alone

Disparity specificity, the degree to which the response is tuned to a specific binocular disparity of the stimuli in the two eyes

Note that the disparity specificity can be tuned to zero disparity, near disparity, or far disparity.

The excitatory connections of receptive fields located in both retinas or retinotopic projections are largely present at birth.^{8,9} However, simultaneous occurrence of patterned visual input to both eyes during the developmental period is necessary to maintain their association.¹⁰⁻¹⁴ For each binocular visual function, there is a period of sensitivity soon after birth during which the formation of receptive fields and other indices of visual processing may be disrupted unless full binocular visual input is available. The period of sensitivity to binocular disruption, produced by patching one eye of an animal

so that there is only monocular visual input, is longer in monkeys than in cats. One index of binocular function is a susceptibility to ocular dominance shifts between the receptive fields of the two eyes. Such cortical dominance shifts seem to start at birth^{15,16} and show susceptibility up to approximately 1 year.^{11,12} Binocular vision could be affected by monocular deprivation up to 2 years of age.^{13,14}

In the developing visual system, patterned visual stimuli seem to act not only as a catalyst but also as a guide in the consolidation, maintenance, and refinement of the neuronal connections of the visual cortex.^{15–20} 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.²¹

A possible function of this plasticity in neuronal properties during early visual experience might be to allow the opportunity to match the properties of feature-detecting cells to the most common features in the animal's visual world, maximizing its capacity for analysis of the more important components of the environment.^{22,23} Also, the ability to make modifications in optimal disparity and the preferred orientation would ensure that binocular cortical cells adopt similar receptive field positions and preferred orientations of the two retinas. Both in immature visual systems and in binocularly deprived visual systems, the binocular responses of cortical neurons are observed to tolerate a wide range of retinal disparity, whereas visual experience narrows this range. Thus, early plasticity seems to be vital to the formation of cells with closely matched receptive field properties in the two eyes, which is a necessary condition to form the substrate for stereoscopic vision. Blakemore and Van Sluyters⁹ propose that “genetically specified, predominately 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.”

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 nuclei, neuronal cell growth is greatly reduced in the laminae with connections to a visually deprived eye as compared with a nondeprived eye.^{10,23} In studies in which one eye was deprived of light for 3 months after birth and was then allowed visual stimulation while the other eye was deprived, the difference in cell size between the lateral geniculate nuclei laminae is decreased and even reversed.²⁴ The two types of retinal ganglion cells and geniculate cells seem to be differently affected by such deprivation.^{25,26} The large cells of the binocular segment (which are found mainly in the pe-

ripheral 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.

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 that is presumed to provide binocularity. The results of monocular deprivation experiments suggest that there is functional competition for effective synaptic input from the two eyes dependent on the actual firing pattern of afferent synaptic fibers, and that this competition represents a crucial process underlying the course and nature of the development of the visual system.^{11–13,19}

The physiologic deficits observed in animals suggest a basis for understanding various human perceptual disorders. Monocularly deprived kittens, for example, do not develop the normal proportion of binocularly driven cortical neurons if the monocular deprivation is imposed during a specific stage in their maturation, which has been determined to be 4 through 12 weeks.^{27,28} 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.^{19,29} Orientation specificity and disparity specificity of the binocular receptive fields for cat cortical neurons are similarly dependent on visual experience in that early postnatal period.^{17–19,29–32} Between the ages of 4 and 10 weeks, 1 week of monocular deprivation is sufficient to produce substantial degradations in stereopsis (as assessed by the difference between monocular and binocular performance on a jumping stand).³³

NORMAL BINOCULAR DEVELOPMENT IN HUMANS

Similar interocular modifications effects have been observed in human development. Four main indices of binocularity have been used with human infants:

1. Accuracy of alignment of the visual axes of the two eyes;
2. Looking preferences by the infant for fixating stimuli containing a binocular disparity over flat stimuli;
3. Binocular facilitation of the visual evoked potential (VEP) amplitude for binocular stimulation to greater than the linear sum of the two eyes' separate signals;
4. VEP responses to changes in binocular correlation and binocular disparity in dynamic random-dot stimuli that are designed to produce no changes that are visible monocularly.

Alignment of the eyes at birth is often imperfect, with *exotropia* (deviation *away* from the nose) occurring in

up to 50% of newborns.^{33A} Irregular fixations and alignment continue for up to 2 months. The eyes should be accurately aligned on targets of interest after this age, however.

Both preferential looking studies^{34,35} and VEP studies³⁶ suggest that the earliest evidence of stereoscopic depth discrimination based on disparity alone occurs at approximately 3 months. What is remarkable about this capability is the rapidity with which it improves, with most infants being able to discriminate as little as 1 arc-minute of disparity by 5 months (see Fig. 4). The same studies show that near-disparity discrimination consistently developed earlier than the far variety. Several techniques^{37–40} have been used to track the development of fine stereoacuity in persons between the ages of 2 and 6 years. Although there are discrepancies up to a factor of 4 at any given age, all agree that stereoacuity improves gradually during this period to close to adult levels by age 6.

The amplitude of the binocular VEP is about the same as the monocular VEP at birth, implying independent processing of the two eyes. An increase in the amplitude of the VEP for binocular relative to monocular viewing is termed *binocular summation*; doubling of the amplitude is termed *full binocular summation* and an increase beyond the range of doubling constitutes *binocular facilitation*. The degree of binocular summation of the VEP increases markedly into the facilitation range at

approximately 3 months and then returns to adult levels of less than full binocular summation by approximately 12 months.⁴¹ This early period of enhanced binocular response appears to coincide with the period of binocular consolidation in humans, which is between 3 and 7 months of age, based on behavioral evidence (see Fig. 4). Correlation-specific VEP responses are not obtained before 2 months of age but are seen in most infants by 3 or 4 months.^{42,43} Thus, the two VEP indices are in fair agreement that the onset of binocular function in human infants occurs at approximately 3 months of age. There is a longer critical period for binocular misalignment in which there is some recovery of binocular function when the eyes of strabismic infants are realigned up to approximately 2 years of age.^{44–46}

ABNORMAL DEVELOPMENT OF BINOCULARITY IN HUMANS

Binocularity and Eye Alignment

The perceptual appreciation of stereopsis involves the analysis of spatially disparate retinal signals from each eye under the condition of binocular single vision. However, about 4% of them are unable to use these disparity cues and perhaps another 10% who have difficulty in judging the type of disparity (i.e., near or far) that they perceive.⁴⁷

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, after adaptation with only one eye, the relative strength of the aftereffect when viewing with the unadapted eye is used as the measure of the degree 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 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 observer's level of stereoacuity. Among the individuals tested in both types of study 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.⁴⁸ The magnitude of the correlations was 0.86 for the tilt aftereffect and 0.75 for the motion aftereffect. This association suggests that both stereopsis and interocular transfer 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 the visual pathway, such that fibers from noncor-

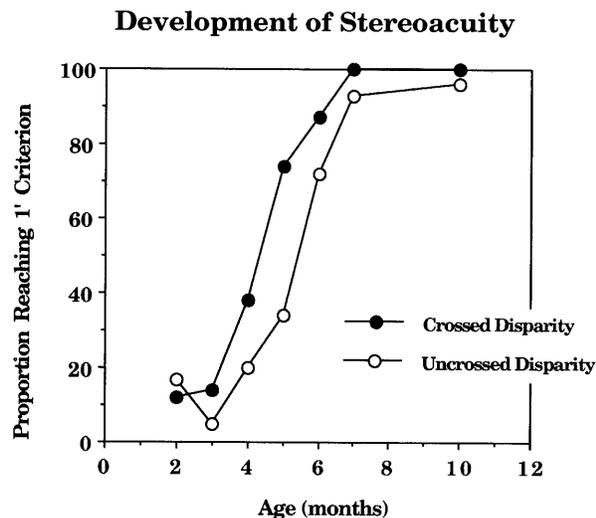


Fig. 4. Development of stereoacuity. Proportion of infants reaching 75% correct performance on a depth discrimination of 1 arc-minute of crossed (filled circles) or uncrossed (open circles) disparity. Note that the crossed disparity performance precedes the uncrossed by approximately 1 month. (Birch EE, Gwiazda J, Held R: Stereoacuity development for crossed and uncrossed disparities in human infants. *Vision Res* 22:507, 1982)

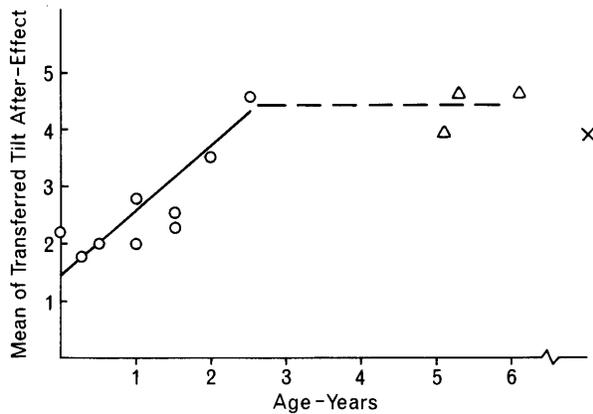


Fig. 5. Interocular transfer of aftereffects as a function of age at onset of strabismus. Strabismus after age 3 caused no reduction in interocular transfer relative to adult levels (x). (Hohmann A, Creutzfeldt OD: Squint and the development of binocularity in humans. *Nature* 254: 613, 1975)

responding retinal areas come together in visual cortex, are known to occur in animals such as the Siamese cat and other albino mammals.^{49,50} Evidence for a similar misalignment in albinotic humans has been obtained from extensive VEP studies.⁵¹

Other studies have shown that a childhood history of strabismus does not eliminate interocular transfer.^{52,53} Two studies involving individuals with an early history of strabismus have used the interocular transfer phenomena to delineate the sensitive period in humans for the development of binocularity. Hohmann and Creutzfeldt (Fig. 5) 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 to 2.6 years of age.⁵³ Additional support for this delineation of a human critical period for the development of binocularity⁵⁴ suggest that the critical period begins several months after birth and extends to approximately 3 years of age. Comparison of functional results from surgical correction of early-onset esotropia with age at correction shows that no patients surgically corrected after the age of 2 years exhibited stereopsis, whereas a high proportion of those who were corrected before that age have demonstrable stereopsis.^{55,56} 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 exhibited and the presumed proportion of binocularly driven cortical neurons.

STRABISMIC AMBLYOPIA

Amblyopia, a loss of spatial resolution without overt retinal pathology, occurs in two major forms differing

in cause and expression.⁵⁷ One is *strabismic amblyopia*, which is the type associated with eye misalignment. Functional competition between the two eyes seems to be a major factor in this condition. Differences between the eyes in image focus (anisometropia) or image magnification (aniseikonia), or partial occlusion of the image in one eye also will lead to a preference for one eye, so that the other eye develops a strabismic misalignment and then amblyopia.⁵⁷⁻⁵⁹ Even though the retinal images may be clear in each eye, one eye may be used for fixation more than the other (e.g., because it has better motor performance), with a resulting amblyopia in the less dominant eye. However, if each eye is used a portion of the time, as in alternating esotropia, asymmetric amblyopia is unlikely to develop. Contrary to the conventional view, however, one report⁶⁰ shows that most alternating esotropes exhibit mild *bilateral amblyopia*, an equal reduction in acuity for both eyes relative to normal, in addition to the expected loss of stereopsis and binocular function. Finally, profound deprivation amblyopia in one eye may lead to strabismus of that eye, for example, in congenital cataract.⁵⁸ Thus, all mixtures of deprivation and strabismic amblyopia occur.

Amblyopia in strabismus is more often associated with eccentricity of fixation than is mild deprivation amblyopia. In approximately 50% of comitant esotropia cases, the position of the retina used for monocular fixation by the amblyopic eye corresponds with its angle of strabismus.⁶⁰

Strabismic amblyopia is frequently seen in infants as young as 4 or 5 months of age; such an *esotropic* eye (misaligned *toward* the nose) may not even be able to fix a target. This fact supports the suggestion⁵⁴ that the "sensitive period" for strabismic amblyopia in humans has its beginning before 5 months. Conversely, amblyopia from a strabismus beginning after the age of 5 or 6 years is rare.

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 condition may be from refractive error (astigmatism, aphakia), from interferences with clear optics (corneal scar, cataract), or from glare degrading the retinal image (aniridia). The visual consequences depend on the severity of deprivation, difference of deprivation between the two eyes, age at onset, and duration before treatment.

Profound defects in retinal imagery from birth (e.g., dense cataract of the lens) affect the visual system so strongly that removal of the cataractous lens after 2 years of age, even given a clear image and occlusion treatment of the good eye (if unilateral), is insufficient to restore useful vision above approximately 20/200 (0.1).

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 diopters (that was present since infancy), when first corrected by glasses at age 5 or 6, typically gives a best corrected vision of 20/100 (0.2). However, development of the vision over 2 to 3 years with corrective glasses results in a visual acuity of almost 20/20 (1.0). Persistence of some amblyopia is found for the more hyperopic meridian in hyperopic astigmatism.⁶²

Besides the severity of blur, the *difference* in image clarity of the two eyes determines the profoundness of amblyopia. It is a common clinical occurrence to see cataracts develop or progress at age 3 or 4 years, resulting in vision of 20/200 or less. When vision is equal in both eyes, amblyopia does not usually occur and 20/20 vision is often restored by surgery. On the contrary, a unilateral cataract of the same severity at such an age is a visual disaster unless rapidly treated, resulting in profound amblyopia.⁶³

If sufficiently severe, a deprivation in infancy cannot be reversed even after a few months of age. Although 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 approximately 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.⁶⁴

An interesting prediction derived from the binocular competition hypothesis of the effects of monocular deprivation is that form deprivation amblyopia should be minimized by the previous occurrence of misalignment between the eyes,⁶⁵ because an early strabismus with alternating fixation generates a strong independence between the cortical representations of the two eyes. The predicted sparing of the deprived eye from profound amblyopia losses has been found in cats⁶⁵ and monkeys.⁶⁶ Paradoxically, therefore, previously strabismus can protect the visual system from the severe effects of monocular deprivation.²⁹

Reports⁶⁷⁻⁶⁹ suggest that deprivation amblyopia can be improved at least transiently in human adults and children by the oral administration of levodopa. Visual acuity, contrast sensitivities, and VEP amplitudes were significantly improved and the size of amblyopic suppression scotoma reduced by administration of this neurotransmitter to the amblyopic patients.

A final aspect of such visual deprivation is a loss of binocular function, even without an amblyopic acuity loss. Even in children as old as 10 to 18 years, the occurrence of cataract by injury may sometimes cause a loss of binocular fusion with resulting diplopia if removal

of the cataract is delayed up to 3 to 4 years. Thus, the period of susceptibility to binocular disruption may persist through adolescence, a much longer period than for strabismic amblyopia.

STEREOSCOPIC VISION

BINOCULAR DISPARITY

Stereopsis was discussed briefly on p. 3, but will now be considered in greater detail. Stereoscopic vision may be defined as the ability to see depth in the third dimension of visual space (i.e., distance from the observer) on the basis of relative image positions of the two retinas. The fact that the two eyes are horizontally separated in space implies that, in general, they will receive slightly disparate views of all objects located at a distance different from the convergence distance. 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 obviously will fall on the fovea in each eye (point F in Fig. 3). There then will be no binocular disparity between the two monocular images. If a second object represented by the arrowhead is now presented at a different distance from the first, a difference in depth may be signaled in two ways: binocular disparity and convergence angle

If we consider the retinal projections of the head and tail of the arrow, there is now a binocular disparity between the projections to the two eyes (see Fig. 3). This disparity can be interpreted neurally as a spatial depth relative to the point of convergence. When the object is in front of the point of convergence, the lines of sight of the monocular images cross before the convergence distance, giving rise to a crossed disparity. If, however, the object were moved away from the observer, 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 a temporal shift for uncrossed disparity do not mean that the images fall on the nasal and temporal retina, respectively, except when the images are at or close to the fovea. Thus, if the near object is viewed at 5 degrees eccentricity to the left, both images will fall to the right of the fovea for all disparities (up to 5 degrees), whether the disparity is near, zero, or far.

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 on the object. The change in vergence angle provides the cue to the new distance of the object, because the binocular disparity is again zero. Thus, vergence angle is a cue to depth that is distinct from, and interacts with, retinal disparity. It may be sensed variously by muscular feedback, by eye movement control signals, or by changes in the vertical disparity fields between the eyes.⁷⁰

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 as small as 10 arc-seconds (0.0028 degrees). 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.⁷¹ Whether monocular information is present or is eliminated, the best observers achieve a 75% discrimination level close to 2 arc-seconds (0.00056 degrees).

This value appears to be one of the finest spatial discriminations of which the human visual system is capable. 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 and also that the discrimination necessitates comparing between two retinas in continuous motion because of eye movements.⁷² 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 inches away, the best stereoscopic threshold corresponds to the appreciation of a depth of one-thousandth of an inch (25 μm). For comparison, this performance is finer than the size of a typical human ovum (100 μm) or the cell body of a typical neuron (50 μm). Conversely, when looking at the horizon, one has stereoscopic discrimination that objects 2 miles away are being nearer than the horizon. This limit allows, for example, stereoscopic discrimination of depth in some types of cloud formations. Contrary to common statements that stereopsis is useful only in the near field, these limits provide useful stereopsis over an extensive range of environmental conditions.

SPATIAL LIMITS OF STEREOPSIS

Although stereoacuity is excellent at the fovea, it diminishes with a steepening function as the stimulus is

moved into the periphery, so that stereopsis becomes very poor beyond approximately 20 degrees eccentricity.⁷³

Just as 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 earlier, depth continues to be perceived well beyond the range of binocular fusion. The perceived depth with disparity is shown as a function of eccentricity in Figure 6. The stimuli were perceived as fused only up to just before the peak of each function. Because it has a logarithmic axis, this graph makes the important point that there is larger region of stereopsis for which the stimuli are diplopic than there is when they are fused. In fact, the greatest perceived depth for each stimulus size is found *beyond* the region of fusion.

Ogle⁷³ 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 regions⁷⁴ (see Fig. 6). It therefore seems more appropriate to designate the two regions as “fused” and “diplopic” stereopsis, thereby avoiding pejorative implications.

Another property that is somewhat related to these two regions is that perceived depth increases linearly with binocular disparity in most of the fused region,

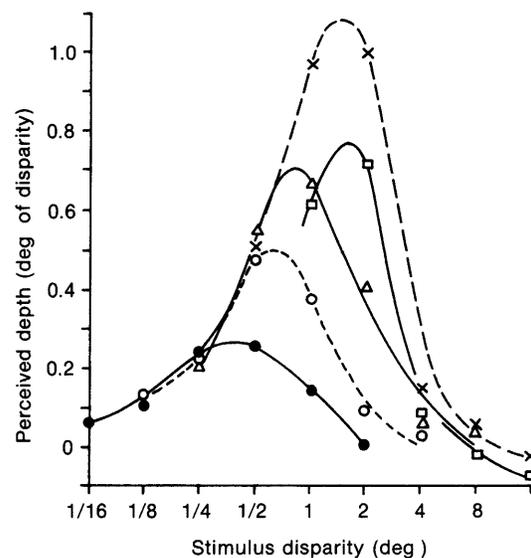


Fig. 6. Relative perceived depth versus stimulus disparity averaged for three observers. Near (convergent) disparities only. Each curve represents a separate bar width: dots, 0.5 degrees; open circles, 0.1 degrees; triangles, 0.2 degrees; crosses, 0.4 degrees; squares, 0.8 degrees. Bar height was fixed at 0.5 degrees. Stimuli were perceived as fused only on the rising portion of the curves. (Richards W, Kay MG: Local versus global stereopsis: Two mechanisms? Vision Res 12:437, 1972)

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.

A Key aspect of Figure 6 is the change in the depth magnitude function for different widths of the text bar.⁷⁴ The maximum depth occurs at disparities varying from 0.5 degrees to approximately 2 degrees; a disparity that can produce no depth impression at all for a small stimulus (e.g., 1 degree) may be optimal for depth perception in larger test objects (see Fig. 6). This result suggests that tests for stereoscopic vision should involve stimuli with a good range of sizes and disparities 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.^{75,76} The maximum disparities for which depth was perceived were inversely proportional to vertical length of the segments over a range from 0.05 degrees to 5 degrees. This behavior 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 seconds to degrees. Thus it is possible to appreciate many aspects of a three-dimensional scene without requiring the order of magnitude of more neurons that would be required for full depth processing to the same resolution as for each eye alone.

A similar limitation occurs in the lower limit of stereopsis, stereoacuity. Mitchell and O'Hagan⁷⁷ 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 approximately 20 arc-minutes. 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.

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.⁷⁸ The basic idea is to present to each eye 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."⁷⁹ 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. Ames was then able to show that the shape of the room was predictably altered by placing different types of magnifying lenses before one eye.

Julesz⁷⁸ demonstrated by means of computer-generated random-dot patterns that it is possible to produce a complete dissociation between the monocular and binocular patterns. If the dot pattern in one eye is completely random, then segments of the pattern may be shifted and rearranged at will but the result always is another random pattern with no hint of the rearrangement that has occurred. If two such patterns are presented dichoptically, however, the visual system is able to use 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 that 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 spiral stereofigure is shown in Figure 7, 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 a necessary precursor 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 cyclopean eye of Hering, which refers to the location inside the head from which binocular visual direction is perceived.) The cyclopean level of processing then provides a benchmark to determine the relative locus of different perceptual functions. For example, Julesz⁸⁰ has found that a large number of visual illusions persist when presented so as to be visible only at the cyclopean

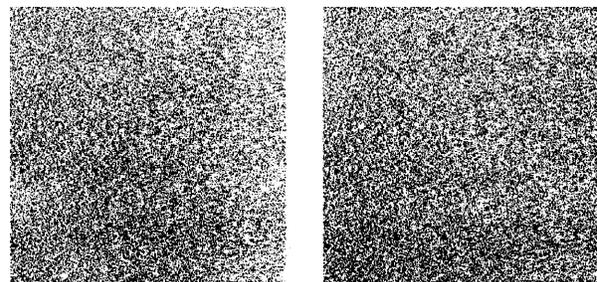


Fig. 7. Random-dot stereogram of a spiral depth figure. When the left and right images are fused stereoscopically, a spiral in depth will appear. These arrays are arranged so that the reader may free-fuse by crossing the eyes to see the spiral pointing upward. (Julesz B: Foundations of Cyclopean Perception. Chicago: University of Chicago Press, 1971)

level. The residual illusion must, therefore, be located in the cortex, rather than processes within the eye.

Clinically, random-dot tests of stereovision are important, because it is impossible to fake the response by looking first with one eye and then the other, because neither contains the stereoscopic figure. However, perception of the form during binocular viewing may be possible by binocular luster alone, so that to demonstrate stereopsis unambiguously, it is necessary to test for the *direction* of depth perception toward or away from the observer. If the patient can distinguish the sign of the perceived depth, it provides unequivocal evidence of a functioning stereoscopic system. With this proviso, well-designed random-dot stereotests can provide the clearest evaluation of stereoscopic ability.

PHYSIOLOGIC 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 identification of similar stimuli and comparison of their minute differences in position 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^{81,82} was in terms of disparities between the positions of the receptive field in each eye for binocular neurons. This analysis now seems more likely to form the basis for binocular fusion only, because the minimum size of receptive fields in monkey cortex seems to be approximately 15 arc-minutes, which would give a range of disparities of approximately half a degree—a far cry from the disparities of a few arc-seconds that can be discriminated behaviorally.

A much more sensitive mechanism of tuning cells for binocular disparity is revealed by looking at binocular interactions during simultaneous stimulation of the two retinal receptive fields.^{83–85} 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 form the first stage of the mechanism by which the cortex processes the hairsbreadth disparities present between the binocular retinal images.⁸⁵

OTHER TYPES OF DISPARITY TUNING

The spatial disparity tuning of cortical neurons is not restricted to neurons with a region of binocular facilitation. Poggio and Fischer⁸⁶ have suggested a classification of binocular interactions of neurons in the cortex of the behaving monkey into four classes, illustrated in Figure 8. Neurons that are predominantly binocular (in the classic sense of having identifiable receptive fields with monocular stimulation of each eye) tended to show either binocular facilitation (A) or a region of binocular suppression (B). Facilitatory neurons could show tuning to near (n) or far (f) disparities relative to the fixation distance (o). More surprisingly, neurons with classically monocular receptive fields showed binocular facilitation for either near (n) or far (f) disparities only. This result is important, because it suggests a neural basis for the separate processes of fine (fused) stereopsis me-

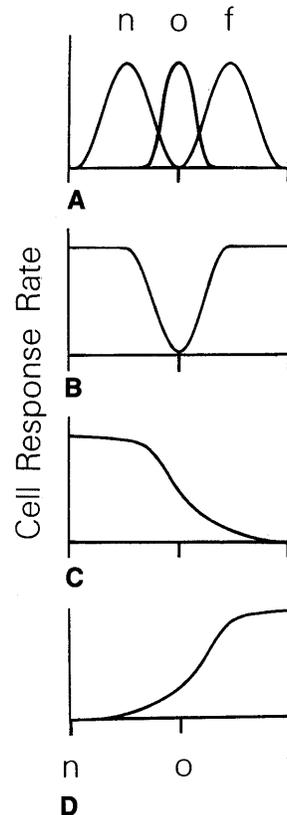


Fig. 8. Four classes of binocular disparity sensitivity in monkey cortex from near (*n*) through zero (*o*) to far (*f*) disparities: **A.** Binocular facilitation. **B.** Binocular occlusion. **C.** Monocular, near. **D.** Monocular, far sensitivities. (Poggio CF, Fisher B: Binocular interaction and depth sensitivity neurons in striate and prestriate cortex of the behaving Rhesus monkey. *J Neurophysiol* 140:1392, 1977)

diated by the facilitatory cells and coarse (diplopic) stereopsis mediated by the monocular cells.

Blakemore and associates⁸⁷ have pointed out that in addition to a spatial binocular disparity, the fact that cortical cells have oriented receptive fields implies that there also may 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 slant in depth. Detection of a depth slant in this manner has the advantage that the orientation cues are independent of the distance (hence, spatial disparity) of the object.⁸⁸

Finally, Pettigrew has reported cells with opposite preferred directions for stimulus motion in the two eyes. Such cells would be well-suited to detect motion in depth toward or away from the observer.⁸⁹ Regan and Cynader⁹⁰ have shown that many cells, particularly those showing binocular occlusion, have a binocular interaction specific for motion in depth—that is, motion in opposite directions of the two retinas.

VISUAL 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. The development of binocularity has been reviewed already in a previous section. There have been three recent techniques reported by which a stereoscopic VEP can be isolated. One method is to determine binocular facilitation in the pattern VEP. A 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.⁹¹ 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 slanted in depth. However, it was not established for what range of conditions or what proportion of the population this effect would be obtained. Srebro⁹² found that some binocular facilitation, in the form of a binocular response greater than the sum of the two monocular responses, occurred in approximately 70% of a normal group. This facilitation was not seen in three patients with small-angle esotropia. However, binocular facilitation in esotropia has been reported by other authors.⁹³

Binocular facilitation in the VEP could be, in general, 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 and associates^{93,94} 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 approximately 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 VEP 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 Spekreijse⁹⁵ using static random-dot stereograms (see Fig. 7). The VEP was recorded in synchrony with a change in disparity of the center region of the stereogram. There already was a large response when the disparity change was in the vertical direction (producing no perceived depth), 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 caused by inclusion of the stereoscopic system. But because 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 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 synchronous VEP is therefore purely cyclopean, and a large disparity-related response can be obtained.⁹⁵ Although the response is obligatorily binocular, there is still an ambiguity as to whether the response originates from the stereoscopic or the binocular fusion system.

When Lehmann and Julesz⁹⁶ introduced the first truly cyclopean VEPs with the use of dynamic random-dot stereographic stimuli, they found a cyclopean response that peaked at approximately 160 msec, as compared with approximately 150 msec for a monocularly visible event.⁹⁷ These results corroborate the psychophysical analysis of a slower response time for cyclopean processing and underline that a detection of a rapid stimulus event does not imply that the detection process is itself rapid. However, it should be noted that the VEP to monocular changes was longer (at 150 msec) than the normal first major peak in the VEP, so there may be some aspect of dynamic random-dot stereogram stimulation that induces inherently slower responses in addition to the extra sluggishness of the cyclopean response.

The same relationship between cyclopean and noncyc-

clopean response speeds was evident in a study of cyclopean depth oscillation in dynamic random-dot stereogram stimulation.⁹⁸ This disparity alternation stimulus produced responses peaking at the low value of approximately 3.5 Hz, and the maximum frequency at which any cyclopean VEP could be obtained was 14 Hz. These low values may be compared with luminance VEPs showing a peak response in the range of 20 to 30 Hz and continuing to respond up to frequencies of 50 to 60 Hz. Thus, the cyclopean response speeds are several times lower than for the luminance-driven responses, again implying that the cyclopean response time is correspondingly slower.

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 two eyes). It is necessary to define more precisely the concept of zero binocular disparity between corresponding points on the two retinas. The simplest definition is based on ocular geometry (see Fig. 2), in which corresponding points on the two retinas are defined as being at the same horizontal and vertical distance (or monocular visual direction) from the center of the fovea of each eye.

Specific to every position of binocular fixation (up–down, left–right, far–near), 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 in space of zero binocular disparity is known as the *horopter* (the “horizon of vision”), a term introduced by Aguilonius nearly four centuries ago.⁹⁹ When defined for point stimuli, this measure forms the *point horopter*, which in general is simply a line in space passing through the point of fixation and connecting all the points in space that project to corresponding points on the two retinas.

TYPES OF HOROPTER

The initial definition of the horopter 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 distortion of binocular correspondence 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.

Moreover, 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*. Such a horopter is based on a higher level percept involving more of the perceptual apparatus, which may add compensations or distortions to the form of the binocular correspondence horopter already defined. The *distance horopter* is therefore not as fundamental a concept as the binocular correspondence type of 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*.

With respect to correspondence horopters, a special case of interest involves the use of disparities in only the horizontal direction, because it is only these disparities that are involved in depth perception. This case 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. The longitudinal horopter is the one most commonly specified in texts and is the main one to have been measured empirically. Whereas the point horopter (measured using points as stimuli) is limited to a single line in space, except for fixation at infinity, note that the longitudinal horopter (measured using vertical line stimuli) is a curved two-dimensional surface in the shape of a cylinder extending from the locations of the two eyes to the fixation point.

A final type of horopter, which is an extension of the empirical horopter, may be specified as the locus of points in space of binocular single vision extending around the horopter. The fusion horopter is the one relevant to ophthalmologic practice because it specifies the boundary between fusion and diplopia anywhere in the visual field, which is a major criterion for visual comfort when viewing with two eyes.

HISTORY OF THE HOROPTER

The concept of corresponding visual directions and the double vision arising from noncorrespondence was recognized by both Euclid and Leonardo. Aguilonius⁹⁹ 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 as a circle passing through the optical centers of the two eyes and point of fixation, as shown in Figure 9 (this construction is usually attributed to Vieth¹⁰⁰ and

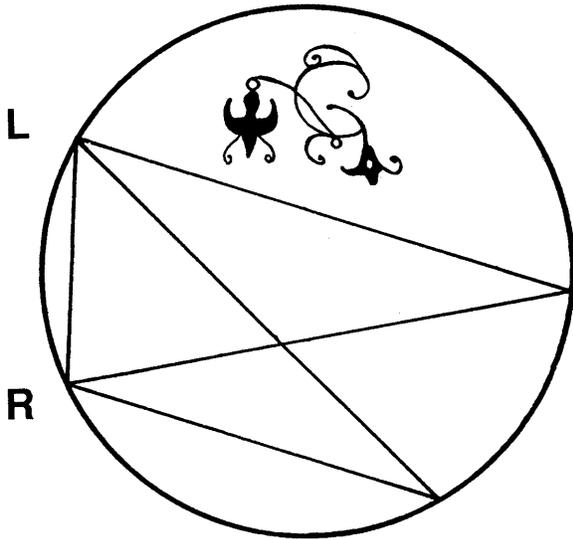


Fig. 9. Vieth-Müller circle from an early diagram by Aguilonius, passing through the point of fixation and the nodal points of the two eyes (*L, R*). All points on such a circle subtend an equal angle at the eyes. Therefore, because the eyes are converged at this angle to foveate at the fixation point, all other points on this circle must be in geometric correspondence.

subsequently Müller¹⁰¹). Interestingly, all this analysis preceded the realization that binocular disparity away from the horopter leads to depth perception, which was first demonstrated in 1833 by Wheatstone.¹⁰²

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 consisting of purely 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 10, it is generally the case that off-axis points project to the two retinas with both horizontal and vertical disparities. The only exception is when the point is at the distance corresponding to the horopter, which would nullify the horizontal disparity. Note particularly the vertical disparity that 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 (see Fig. 10). Thus, all off-axis points (except for fixation at infinity) project with some vertical disparity

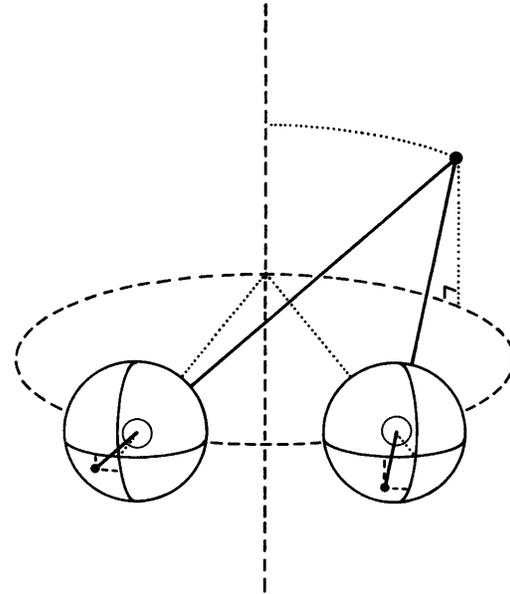


Fig. 10. For convergence at any distance other than infinity, all points that do not lie on the Vieth-Müller circle or the vertical horopter line project to the retina with either a vertical disparity or both a vertical and horizontal disparity. Dashed lines show geometric horopter for symmetric fixation (*dotted lines from foveae*). Full lines represent light rays from a selected point in space. 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.

to the two eyes. These points therefore are excluded from the horopter of zero disparities.

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 Prevost.)¹⁰³ 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.

At the same time, there is another component of the symmetric line horopter corresponding to the circle designated as the Vieth-Müller circle (although it was first specified by Aguilonius⁹⁹). This geometric horopter circle passes through the point of fixation and the nodal points of the two eyes. All other points in space project with some horizontal or vertical disparity to the two eyes. To reiterate, the point horopter for symmetric fixation in the visual plane therefore consists of a vertical line and a horizontal circle (see Fig. 10).

THE POINT HOROPTER WITH ASYMMETRIC CONVERGENCE IN THE VISUAL PLANE

Asymmetric 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 horopter circle would imply that, as the eyes fixate at different points around a given horopter 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 horopter circle, rather than following the position of the foveae (Fig. 11A). This invariance 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 to the extent that the center of rotation differs slightly from the nodal point of the eye). Thus, in gaze to the right, the foveal image in the right eye is magnified relative to the left 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. 10). The direct consequence of this geometry is that, in eccentric fixation, the regions

immediately above and below the fovea have an inherent vertical disparity that must affect the stereoscopic and fusion abilities (see Fig. 18).

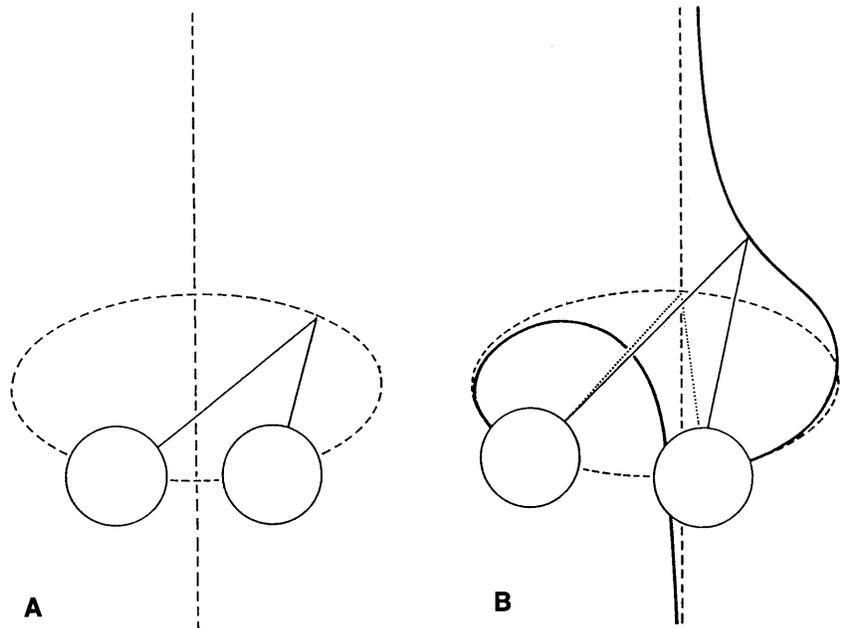
THE GENERALIZED POINT HOROPTER IN ASYMMETRIC CONVERGENCE

Finally, the most general case is to allow fixation at any point, which will include asymmetric convergence away from the visual plane. This case was developed in detail by von Helmholtz¹⁰⁴ and is a curve of the third degree, which forms a single loop spiral (see Fig. 11B). 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 \pm infinity. 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 MEASUREMENTS OF THE HOROPTER

Although it generally is true that corresponding points in the retinas project to the same region of visual cortex, there are two important ways in which a precise relation-

Fig. 11. A. Geometric horopter with asymmetric fixation (*dashed lines*). 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 lines*).



ship does not hold. One is that many neurons in the primary visual cortex respond best to stimuli with some nonzero binocular disparity.⁸¹ This spread makes the physiologic definition of zero disparity a statistical question of the distribution of optimal disparities, rather than a precise correspondence. The other is that there are systematic distortions between the two eyes in the cortical mapping.

THE VISUAL PLANE

As mentioned previously, the measurements of the horopter by Hering and Hillebrand (which were made only within the horizontal visual plane) showed a consistent deviation from the geometric Vieth-Müller circle, whether the horopter was measured in terms of equal visual direction or by the more perceptual criteria of the range of fusion or equal perceived distance.^{105,106}

Ogle^{107,108} 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 a circle, ellipse, straight line, or hyperbola, depending on the radius of curvature at the point of fixation. If the Hering-Hillebrand deviation from the horopter 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 geometric horopter that the empirical horopter will remain a circle as fixation distance varies.) A family of curves for different fixation distances is shown in Figure 12, illustrating how the empirical horopter progressively curves away from the observer as fixation distance increases.

FIXATION AT INFINITY AND THE 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 case therefore is only one in which the point horopter can be considered a plane. However, there is already a complication. Volkmann¹⁰⁹ and von Helmholtz¹⁰³ compared the vertical meridian between the two eyes and found that with fixation in the primary position there is a tilt of approximately 2 degrees when the vertical of one eye is matched to the vertical in the other, whereas no such tilt appears in the horizontal direction. Because this tilt is anisotropic to the vertical direction, it is best described as a *shear* of retinal correspondence.

The von Helmholtz shear completely rotates the plane of the empirical point horopter away from the geometric construct. Figure 13A shows the projection of the vertical correspondence meridians of the two eyes through the pupils with parallel symmetric fixation. Each set of

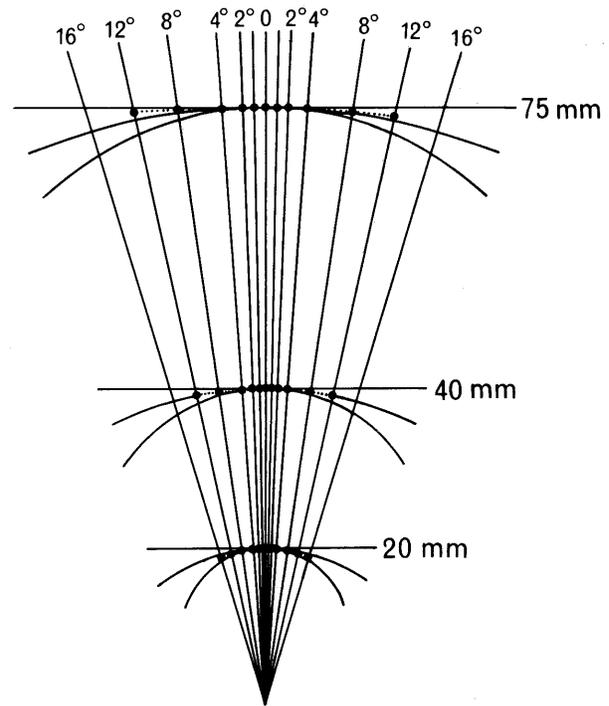


Fig. 12. Hering-Hillebrand deviation from the geometric horopter circle. Note the change in form of the deviation with fixation distance. (Ogle KN: *Researches in Binocular Vision*. Philadelphia: WB Saunders, 1950)

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-degree tilt of the vertical midlines that the line in which the planes meet will vary in angle according to fixation distance (see Fig. 13B). For fixation at infinity, the planes will meet in a horizontal line running below the eyes, approximately 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. Therefore, von Helmholtz suggested that the 2-degree shear has an adaptive function of removing the horopter from correspondence for 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 consider three binocular abnormalities that affect the form of the horopter: fixation disparity, aniseikonia, and abnormal retinal correspondence.

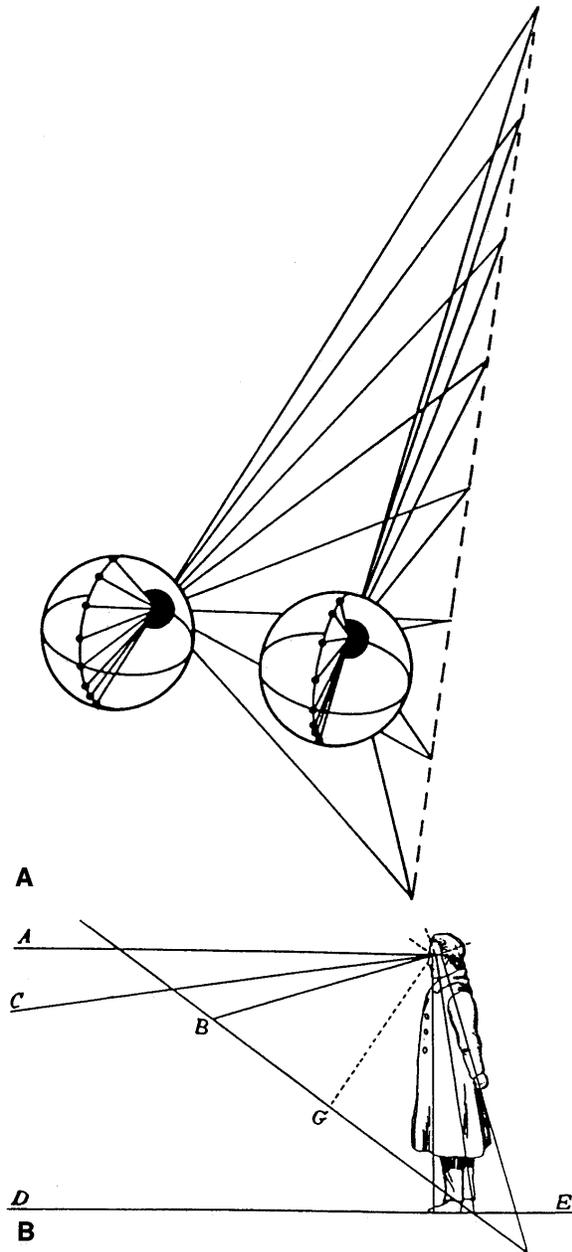


Fig. 13. A. Projection of vertical meridian, showing that if the meridians are aligned with each pupil they must project in two planes that meet in a straight line, rather than any kind of curve. In addition, if the vertical meridians are slanted relative to each other, the line in which they meet will be slanted 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 degrees, 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)

Fixation disparity is a very straightforward concept; it simply means that the observer is fixating binocularly with a slight but consistent 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 shift may arise from a small foveal scotoma or from an oculomotor imbalance that 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 Ogle¹⁰⁷ on his own eyes (Fig. 14A).

The oculomotor generation of fixation disparity may arise from a normal, or physiologic, basis or because the muscle control system has developed to produce an ocular misalignment even under optimal conditions.¹¹⁰ The physiologic fixation disparity arises if the fixated object is present at a distance significantly in front of or behind the position of resting vergence, which is usually between 1 and 2 meters from the eyes. Oculomotor imbalance is a tendency for the eyes to converge to an angle very different from the normal range when fixation stimuli are absent. This condition is known as either esophoria or exophoria, according to whether the eyes tend to become more crossed or more uncrossed than the normal range, respectively. The stresses such an imbalance puts on the fixation system reveal themselves as either near or far fixation disparities, respectively, when a fixation object is present.

Aniseikonia, the unequal magnification of images in the two eyes, occurs principally as a result of unequal optical refractions in the two eyes (or even unilateral removal of a lens; *aphakia*). Such a magnification difference may occur not only in spherical error but also in terms of the strength or axial orientation of cylindrical errors. When the refractive error is corrected, there may be a residual difference in the magnification of the two images. This difference distorts the shape of the entire horopter, and the distortion may become so large that binocular fusion and stereopsis become practically impossible.

The form of the horizontal plane of the empirical fusion horopter with 3% magnification of the image to the right eye¹⁰⁸ is shown in Figure 14B. The curvature of the horopter now has a backward slant to the left. As a quantitative example, at an observation distance of 1 meter, a magnification difference of only 5% will produce a slant of as much as 50 degrees, which may make normal binocular fusion and stereopsis very difficult, and even lead to strabismus and amblyopia if it occurs in a young child. In fact, Peters¹¹¹ found a loss of stereopsis when artificial aniseikonia was produced with a

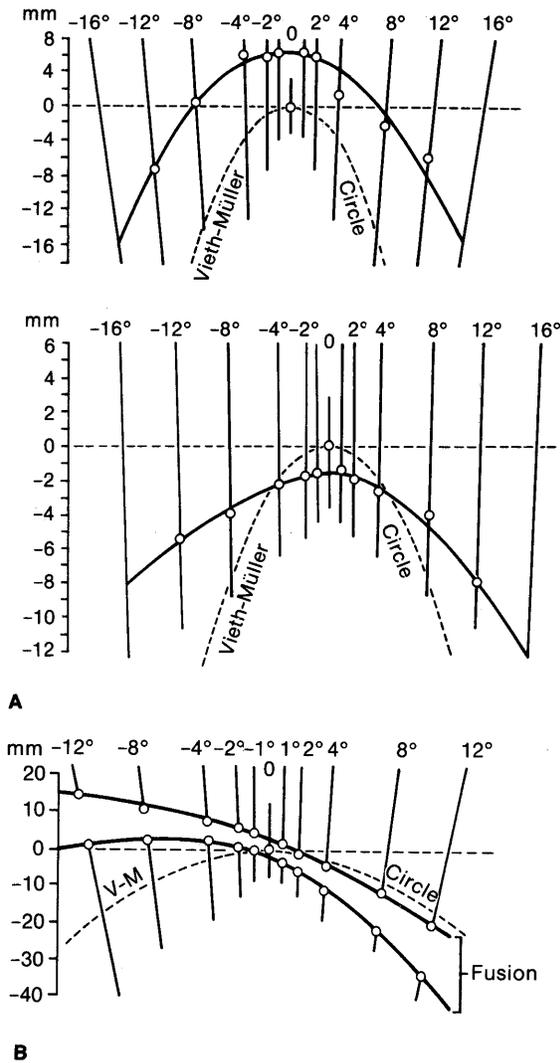


Fig. 14. A. Effect of fixation disparity on the position of the horopter circle. *Upper panel:* Exodeviation. *Lower panel:* Esodeviation. **B.** Effect of aniseikonia (differential magnification of image in the two eyes) on the form of the horopter circle, which becomes an ellipse, delineated here by the limits of the fusion range on either side of the horopter. (Ogle KN: *Researches in Binocular Vision*. Philadelphia: WB Saunders, 1950)

magnitude as little as 1 diopter difference in refractive power between the two eyes.

Anomalous retinal correspondence is a condition that occurs in certain types of strabismus, wherein equal visual direction (correspondence is established for certain retinal regions that are disparate in normal vision. Consider the case of concomitant esotropia with the visual image symbolized by the line *abcde* at the top of Figure 15. This image projects optically to each eye (symbol-

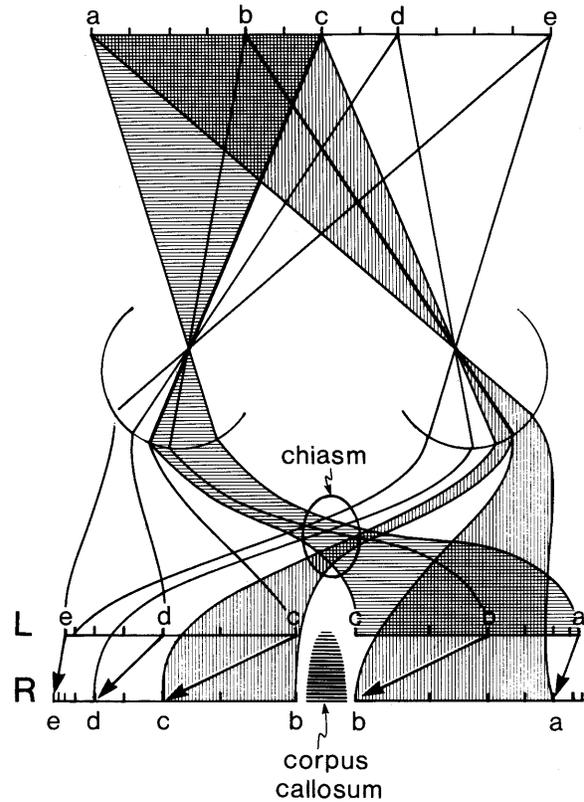


Fig. 15. Diagram of neural connections in anomalous retinal correspondence. Equally spaced points *a*, *b*, *d*, and *e* around point *c* in visual space project through the nodal points of the eyes onto the retinas. Note that the projection onto the cortex gives preferential weighting to the foveal region (around point *c*). Development of anomalous retinal correspondence in strabismus gives distorted match of left to right connections from left and right eyes. Region *abc* from the right eye (*stippled*) has anomalous connection relative to region *abc* from the left eye (*cross-hatched*).

ized by its eye cup) and thence by neural pathways to the visual cortex (two levels of which are depicted at the bottom of the figure). 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. Although not in the exact corresponding areas, these projections of the left eye can potentially reconnect with the normal cortical areas (see Fig. 15, arrows). In fact, the reconnection may be at a higher level of processing, but the concept is equally applicable. The region *cb* in one eye potentially can 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 anomalous retinal correspondence to complete the horopter in this anomalous region.¹¹²

One important feature of early esotropia is a profound

suppression of the perception from the central region of whichever eye is not fixating. This effect 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 (see Fig. 15). The stretch from *b* (right eye) to *h* (left eye) is a long one in the cortex, although it is a small one in angle of vision. The adaptation is difficult here, so the interconnection is often not made and suppression of one image results. However, the stretch from *a* to *a* and from *e* to *e* is shorter in the cortex, and binocular 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. Anomalous retinal correspondence and suppression are adaptations that do not take place when the misaligned projection occurs in adult visual cortex.

CHARACTERISTICS OF AMBLYOPIA AND STEREOACUITY DEFICITS IN BINOCULAR VISION DISORDERS

Amblyopia is typically considered to be a deficit in spatial acuity with no detectable organic cause. In a large-scale study, McKee, Levi and Movshon¹¹³ confirmed that the two main causes of such deficits are reduced optical resolution in one eye (anisometropia) and loss of binocular coordination (strabismus). Deficits of binocular vision affected the letter and vernier acuity more than contrast sensitivity, anisometropia typically had a greater effect on contrast sensitivity, and anisometropia typically had a greater effect on contrast sensitivity. Interestingly, the deficits in depth perception that accompany amblyopia seem to extend to depth from nonbinocular cues. Thompson and Nawrot¹¹⁴ found that amblyopic observers perceived less depth than normal from purely motion parallax displays, implying that the whole system for processing depth from any source is disrupted by binocular vision deficits.

One hypothesis for the particular losses in strabismic amblyopia is a reduction in the density of cortical neurons that are driven by the amblyopic eye, the cortical undersampling hypothesis of Levi and colleagues.^{115–121} To assess the spatial sampling with maximal retinal contrast, Sharma, Levi and Colletta¹²² imaged gratings on the fovea of each observer using a laser interferometer. Orientation discrimination by strabismic

amblyopes implied that the sampling frequency is 2–6 times lower than the sampling frequency of the foveal cones, suggesting sparse cortical sampling in the foveal representation of the amblyopic eye.

However, there is also a factor of suppression of the amblyopic eye by the stronger fellow eye. Norcia, Harad and Brown¹²³ used a visual evoked potential technique to evaluate the separate effects of the two eyes during binocular vision in patients lacking normal stereopsis. The two eyes were stimulated at different temporal frequencies, providing a label by which the activity associated with each eye can be tracked during binocular interactions. Although they had lost the response component representing facilitatory binocular interactions, these patients retained suppressive binocular interactions. The consequent dichoptic suppression was stronger with the masker in the dominant eye, as expected if this inhibitory binocular interaction forms the basis of clinical suppression.

Amblyopic losses with moderate levels of both spherical and cylindrical types of anisometropia^{124,125} are accompanied by deficits in stereoacuity. Of the varieties of strabismus, intermittent exotropia does not degrade stereopsis and can be successfully treated with surgery in most cases.¹²⁶

Infantile esotropia, however, has a profound effect on stereoacuity^{127,128} that is only partly relieved by corrective surgery within the first 2 years after birth.¹²⁹ For congenital esotropia, the two main prognostics for recovery of stereopsis after surgery are smaller preoperative angle of deviation and earlier surgical intervention.¹³⁰ In acquired esotropia, however, the only prognostic factor is the preoperative angle of deviation.¹³⁰ Congenital cataract also severely affects stereoacuity, although compensating for both strabismus angle and the acuity loss of amblyopia by aligning coarse stereograms on the visual axes revealed residual stereopsis in a small proportion of cases, particularly those with later onset.¹³¹ Early treatment was successful in recovering stereopsis in a substantial proportion of congenital cataract patients,¹³² rising to a 50% level with the inclusion a partial occlusion regimen.¹³³

BINOCULAR FUSION

CLASSIC THEORIES OF BINOCULAR FUSION

There have been four classic approaches to understanding the binocular fusion of stimuli in the two eyes into a single percept: (1) the synergy hypothesis; (2) the local sign hypothesis; (3) the eye movement hypothesis; and (4) the suppression hypothesis. Each is subject to serious misgivings, and all have essentially been rendered obsolete by neurophysiologic data on binocular responses.

Because elements of several of the classic hypotheses are incorporated into the physiologic hypothesis, they are briefly described.

In the synergy hypothesis, Panum¹³⁴ originated the suggestion that binocular fusion is caused by the “binocular synergy of single vision by corresponding circles of sensation.” By this description, 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 known as Panum’s area. Nevertheless, information as to which point is stimulated within the “corresponding circle of sensation” is not lost but remains available in the visual system for the perception of depth. This last stipulation is necessary because, although the range of binocular disparities allowing fusion is typically in the region of 10 to 20 arc-minutes, 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.¹⁰⁵ 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 thus the image is seen as single. The finer resolution of stereoscopic depth is treated by positing a further “depth sign” that 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.¹³⁵ 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; instead, rivalry and suppression occur between the dot and line in the region of correspondence. This result is contradictory to the local sign hypothesis, because each stimulus should have the same local sign at this point and therefore should be perceived as fused.

As an alternative, von Helmholtz¹⁰⁴ proposed an *eye-movement hypothesis* of fusion, based on the idea that small eye movements make 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, however, by the fact that stereoscopic depth

has a much finer resolution than fusion, whereas the eye movement hypothesis, implies that fusion would have a similar resolution.

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 revived by Verhoeff.¹³⁵ 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 disparate 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 in which 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, although each hypothesis may have some degree of validity in special circumstances, none provides 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.¹³⁶ An initial version of the physiologic hypothesis⁸³ is based on the distribution of disparities of the binocular receptive fields. In its current form, this hypothesis would use the neurophysiologic data on different types of binocular neurons in the visual cortex. Hubel and Wiesel¹³⁷ 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^{81–86} 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 also in all retinal directions. The extent of binocular interactions and problems with 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 difficult 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. 16). 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, in which it is simplest to assume that the visual direction 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 between the two images breaks and diplopia is perceived. When the stimuli are at corresponding points, the three classes (binocular corresponding neurons and monocular right and left neurons) derived from a single visual direction label are not in 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 each are stimulated for a visual direction slightly to either side of the mean visual direction for the binocular disparate neurons (see Fig. 16). Thus, the two monocular visual directions, which would be discriminately 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, a point is reached at which the disparity is increased beyond the range in which the binocular response can be integrated with the two monocular responses. Now each monocular response is associated

with a different visual direction; therefore, two separate stimuli are perceived in diplopia. What happens to the visual direction associated with the binocular disparate neurons? 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 the Stereopsis heading, the binocular disparate neurons probably operate in a small range, essentially only in the region of fusion. Larger 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.

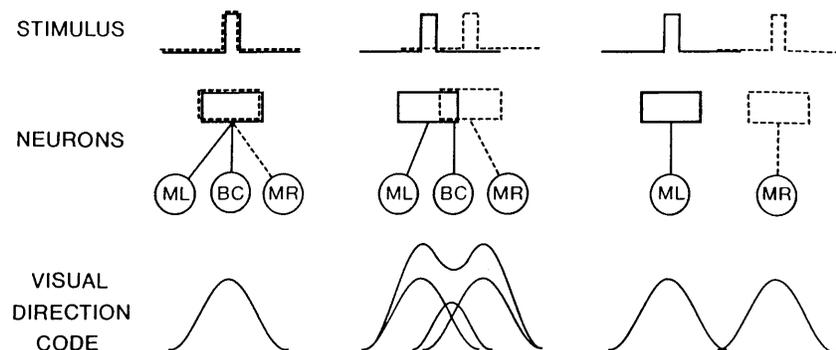
RETINAL ECCENTRICITY, FUSION, AND CYCLOFUSION

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 eccentricity⁷⁹ is shown in Figure 17A. Thus, “Panum’s area” is not of fixed size but increases approximately 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 proportional 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 also is adaptive in terms of the binocular environment. Figure 17B shows the disparities produced by binocular viewing of a plane optimally slanted 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 looking at a flat-screen monitor at a comfortable distance. The disparities present at large distances from fixation are substantial and increase roughly in proportion to degree of eccen-

Fig. 16. Model of binocular fusion and diplopia considered from the point of view of three classes of cortical neuronal receptive field with similar visual directions—monocular left eye (ML), monocular right eye (MR), and binocular corresponding (BC). Stimulus inputs to these receptive fields are shown as full (left eye) and dashed (right eye) lines for zero, small, and large binocular disparities. Third line shows individual and combined visual direction codes for the three types of neurons.



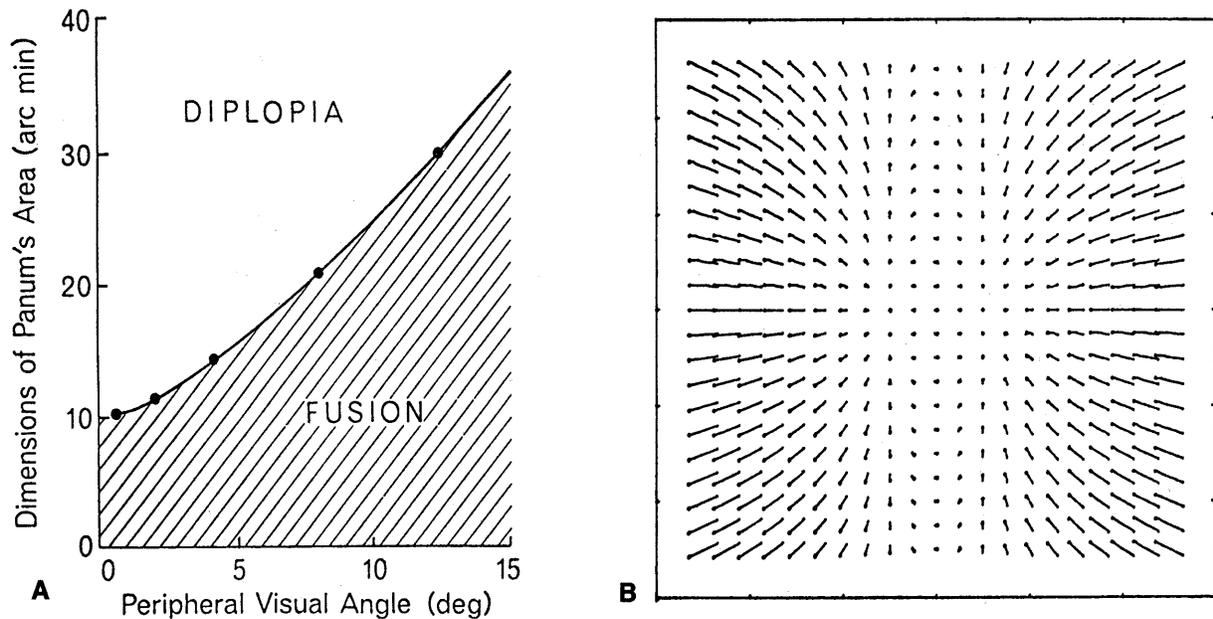


Fig. 17. A. Variation in Panum's area of binocular fusion with retinal eccentricity. **B.** The field of geometric disparities of a flat plane viewed at 20 cm and slightly in front of the fixation point. This shows that relatively large disparities can occur in peripheral regions under conditions that might occur while reading or writing. (**A.** Ogle KN: On the limits of stereoscopic vision. *J Exp Psychol* 44:253, 1952; **B.** Nakayama K: Geometric and physiological aspects of depth perception. *Proc SPIE* 120:2, 1977)

tricity. 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 arc minutes 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 degrees.

FUSION HOROPTER

As an application of this idea of the range of sensory fusion, one can measure the range of fusion around the horopter of corresponding points to show the total region of space before the observer within which point stimuli will appear fused. This empirical fusion horopter is depicted in Figure 18 for the special case of symmetric fixation in the visual plane (A) and the general case of asymmetric fixation of the visual plane (B). Note that the fusion horopter runs wide of the geometric Vieth-Müller circle because of the Hering-Hillebrand deviation.

The case for asymmetric fixation (see Fig. 18B) is based on the von 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. 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. Suggestions¹³⁸ that the fusion horopter has the form of a torus are based on the incorrect assumption that the horopter is defined by the trajectory of the Vieth-Müller circle as the eyes rotate vertically, and is not empirically validated.

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. In this manner, fusion depends on the spatial extent of the stimulus.

More systematically, Tyler⁷⁶ has examined fusion as a function of size of the waves in a sinusoidal line stimulus. 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 re-

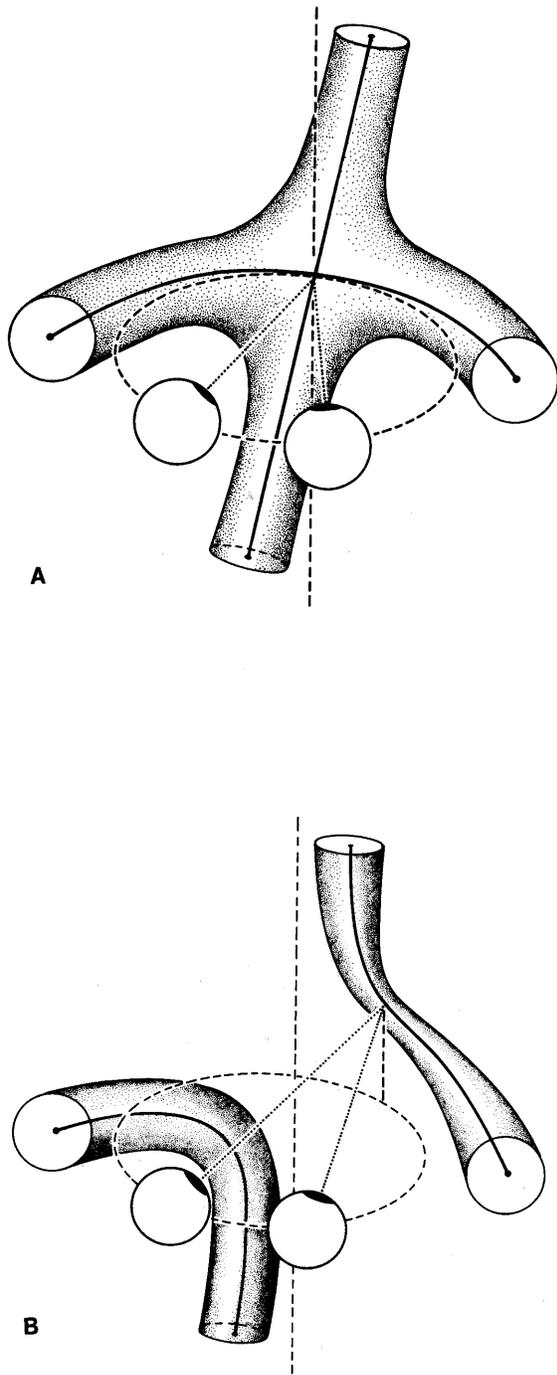


Fig. 18. A. The empirical fusion horopter for symmetric fixation in the visual plane. Note the spread away from the geometric horopter (*dashed line*) due to the Hering-Hillebrand deviation and the vertical tilt caused by the Volkmann-Helmholtz shear of the vertical meridians. **B.** The generalized empirical fusion horopter for any other fixation point. Note that asymmetric fixation produces a dramatic thinning of the fused region near the fixation point.

mained reasonably constant (Fig. 19), but when the wavy stimulus lines were vertical, Panum's area varied dramatically with the size of the waves (or spatial frequency¹). The maximum retinal disparity could be as much as 1 degree when the waves had a period of 30 degrees per cycle. These variations all occurred with the stimulus passing through the fovea.

Thus, the traditional concept of Panum's area as a fixed property or a particular retinal region must be replaced by the awareness that 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; the depictions in Figure 18 provide only 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 FUSION

One interesting aspect of the fusion limit is that it is established in a very short time. Von Helmholtz¹⁰⁴ had

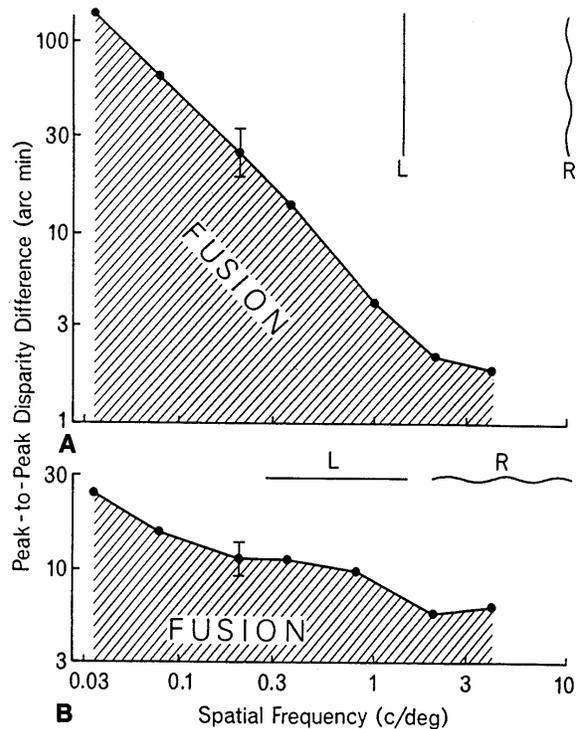


Fig. 19. Fusion limit as a function of stimulus pattern of a sinusoidal line (*inset*). **A.** For horizontal disparity (*upper inset*), fusion limit increases for stimuli with large cycles and decreases for stimuli with very small cycles. **B.** For vertical disparities (*lower inset*), the fusion limit remains much more constant. (Tyler CW: The spatial organization of binocular disparity sensitivity. *Vision Res* 15:583, 1975)

experimented with fusion in stereograms illuminated by a (microsecond) electric spark. Woo¹³⁹ examined the effect of duration systematically and found that fusion appeared to be complete by approximately 30 msec. This duration 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.

However, the fusion of complex targets is a very different matter. It is possible to generate fields of dynamically changing random dots that are identical in the two eyes (and can be perceived as fused) or dots whose positions are spatially uncorrelated between the two eyes, which are perceived as entirely unfused. Fusion will persist even though the dots are rapidly changing, providing they always occupy instantaneous 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 Tyler¹⁴⁰ 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 measured the time required to detect a break in fusion immediately followed by a return to the fused stimulus (identical fields), the duration was about ten times shorter. 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. Some extreme nonlinearity of binocular temporal processing would be required to account for this bias between the two types of binocular correlation threshold.

VISUAL EVOKED POTENTIALS AND FUSION

Many types of binocular interaction are reflected in the VEP recorded from the human scalp. These fall into the categories of binocular summation, binocular rivalry and suppression, and stereopsis, each of which is considered separately.

VEP amplitude shows partial binocular summation under most conditions of binocular corresponding stimulation,¹⁴¹⁻¹⁴⁴ whether the stimulus is a flickering field or an alternating pattern of some kind. 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 cited studies report partial binocular summation on the order of 1.4 times greater than the mean monocular response, both for high-contrast stimulation and close to

threshold response. However, these studies all involved transient VEPs measured at a single peak. An earlier study by Spekreijse¹⁴⁵ had used sinusoidal flicker of a uniform field for the stimulus. This study revealed that saturation of the VEP occurred in many circumstances high-amplitude stimulation, 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 work¹⁴⁶ using sinusoidal patterns flickering in counterphase 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 of the binocular response. Such binocular facilitation is presumed to reflect the activity of stereoscopic neurons.

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 six classes of percept that are obtained, depending on the degree of noncorrespondence between the stimuli:

1. Depth with fusion: The fused binocular image is perceived in depth relative to its background
2. Depth with diplopia: The disparity becomes great enough for the stimulus to split into separate monocular images, but paradoxically their depth continues to increase even while being seen as double
3. Diplopia without depth: With further disparity increases, the perceived depth of the double image declines back to the level of the background
4. Dichoptic fusion: If dissimilar images to the two eyes overlap, they will be seen as their additive sum if they are of low effective contrast
5. Binocular rivalry and suppression: At high-contrast, rivalry alternation between the two monocular images sets in
6. Binocular luster: If the images are of opposite contrast in the two eyes, they will be with a kind of lustrous shimmer as though both light and dark are simultaneously visible

The first two classes are dealt with in the section on stereoscopic vision. They are not generally referred to as dichoptic, because the two retinal patterns are sufficiently similar as to be combined into a unified impression (particularly for fused stereopsis). The latter four 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 therefore

covers the remaining topics: dichoptic fusion, binocular rivalry, binocular suppression, and binocular luster.

DICHOPTIC FUSION

The first reports of fusion between dichoptically dissimilar images^{141,142} were obtained with very brief exposures of the dichoptic stimuli.^{147,148} High-contrast orthogonal gratings in the two eyes appeared to form a fused dichoptic plaid, but only for durations shorter than 150 msec.¹⁴² Until recently, the effect of contrast of binocular combination had not been explored. Liu and associates¹⁴⁹ found that orthogonal dichoptic gratings show complete perceptual summation for periods of up to 30 seconds after stimulus onset. The dichoptic summation lasts the longest for high spatial frequencies and near threshold contrasts, but at medium spatial frequencies (e.g., 3 cycles per degree) and 10% contrast, dichoptic summation into a perceived plaid was still obtained for an average of 5 seconds, which might be a typical trial duration for a free-viewing task. This ability, hitherto unrecognized in the human brain, may explain the role of the 50% of primate cortical cells that are binocular and have circularly symmetric receptive fields that cannot discriminate the difference between the bar orientations in the two eyes.¹⁴⁴

BINOCULAR RIVALRY AND SUPPRESSION

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 (Fig. 20).

Binocular rivalry fluctuations are similar in many re-

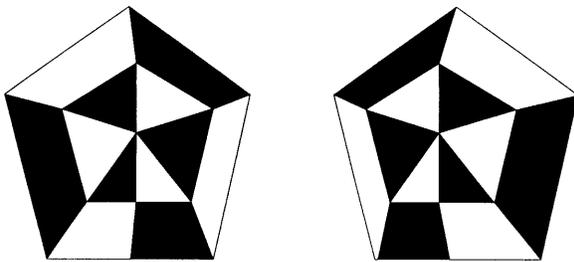


Fig. 20. Stimulus demonstrating strong binocular rivalry when left panel is viewed by left eye and right panel is viewed by right eye in the same retinal location. The opposite contrasts in each eye tend to switch at random between perception of the light and dark phases. They also exhibit a lustrous, shimmering quality. Note that there is a disparity between the center pentagons in each eye that may be perceived as a relative depth signal even though the contours are of opposite contrast at all points in the figure.

spects to fluctuations of attention and are widely supposed to be under voluntary control. Actually, a number of studies^{150–152} has found that there is little voluntary control over which eye dominates at any given time. 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.^{153,154}

A series of studies by Fox and co-workers on the characteristics of binocular rivalry has 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, the result is quite significant in determining the processes of binocular cooperation and their breakdown in pathologic conditions.

Interocular suppression has a number of interesting characteristics. The suppression state is inhibitory. Test stimuli presented during suppression are attenuated relative to the same stimuli presented during dominance or during nonrivalry conditions. This attenuation occurs 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.^{154–158}

The magnitude of the inhibitory effect varies among subjects and with stimulus conditions but is generally approximately a factor of three, a value frequently observed in studies of saccadic suppression and visual masking. The inhibitory effect of suppression endures throughout the duration of the suppression phase, and the magnitude of the inhibition remains constant.¹⁵³

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 degrees and of a factor of two or more in frequency remain undetected.¹⁵⁴

These studies suggest that rivalry is a process that is 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.^{147,155–157}

Finally, two interesting experiments have explored the relationship between aftereffects of visual adaptation and rivalry suppression. Examples of visual aftereffects are the perceived motion obtained as an aftereffect of adaptation to a moving display, threshold elevation and perceived spatial frequency shift after adaptation to a grating. Perceptual occlusion of the stimulus during binocular rivalry did not affect the strength of these aftereffects, whereas equivalent physical occlusion of the stimulus reduced the aftereffect dramatically.¹⁵⁸ In effect, the brain was adapting to an invisible stimulus. Because these aftereffects are almost certainly cortical, binocular rivalry must be occurring at a higher level in the cortex.

VISUAL EVOKED POTENTIALS AND BINOCULAR RIVALRY

VEPs to pattern reversal can be recorded during binocular rivalry conditions. Cobb and colleagues¹⁶⁷ used a stimulus with vertical bars to the left eye and horizontal bars to the right eye, with pattern reversals at 12 Hz, 180 degrees 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 and co-workers¹⁶⁸ 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 because 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 binocular rivalry operates before the site at which the pattern VEP is generated (at least for low frequencies of alternation). 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 percept that can occur with noncorresponding stimuli. It occurs in areas of uniform illumination in which the luminance or color of the reflected light is different for the two eyes. It was described by von Helmholtz¹⁰⁴ and Panum¹²⁹ as a kind of lustrous or shimmering surface of indeterminate

depth see (Fig. 20). The lustrous appearance of surfaces like a waxed tabletop or a car body is largely attributable 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, both of which may be depicted in a photograph corresponding to the image by a single eye. Viewed binocularly, the lustrous surface appears to have a translucent quality of depth due to diffusion from the surface as well as the partial reflected 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. 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.^{78,140} 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 an exclusively binocular (cyclopean) task and suggests that binocular luster is a phenomenon worth further study.

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