Introduction

The geometry of binocular vision has provoked interest for several centuries. At the beginning of the seventeenth century, Father Franciscus Aguilonius (1613) appreciated that the images projected into the two eyes were slightly different, by virtue of the difference between each eye’s viewing angle. He used this fact to develop an analysis of the positions in space that would fall on corresponding points in the two eyes. But the role of binocular disparity in depth perception was not appreciated until the nineteenth century expansion of interest in vision, and it was this conceptual advance which brought the analysis of binocular geometry into prominence. This chapter will review physiological and geometric analyses of binocular projective space, emphasizing their role in binocular fusion and depth perception.

Definitions

Binocular Visual Direction

Visual direction is the perceived frontal plane position of a stimulus in relation to the observer; up, down, left or right. When specified with the eyes in their primary positions (i.e. looking straight ahead), visual direction provides the basic metric of the visual position sense. Visual direction can be specified either for the binocular perception of the stimulus or for the perceived monocular images, if there is sufficient binocular disparity between the two monocular images for them to be perceived separately (see below). Monocular points which project at the same perceived visual direction in the two eyes are called corresponding points. They define zero binocular disparity, and are considered to project to the same region of visual cortex.

There is a limited set of physical points in space which project to corresponding retinal points and which define the horopter for a given fixation position.

Sensory Fusion and Diplopia

If the images in the two eyes are very similar and one is moved slightly to produce a small binocular disparity, the binocular stimuli will still be perceived as fused into a single image. The range of binocular disparities over which the image remains fused and single has been classically known as Panum’s (1858) fusional region. Beyond this region the stimuli to each eye are perceived separately. This perception of the stimulus as doubled is known as diplopia.

Vergence Angle

A second aspect of binocular physiology which relates to space perception is the direction in which the two eyes are pointing. If we define the visual axis of an eye as the line passing through the fovea and the mean optical nodal point of the eye, then the angle between the two visual axes is the vergence angle. This angle is convergent if the eyes are pointed so that the visual axes cross closer than infinity, otherwise it is divergent. Wherever the visual axes cross is, by definition, zero disparity, and may be considered the origin of binocular visual space. The vergence angle affects many aspects of horopter which are considered in this chapter.

Binocular Visual Direction and the Horopter

Perceived Visual Direction

The study of the perceived visual direction of a binocular image has a long history dating back to Hering (1864).
Consider a situation in which point light sources are projected to corresponding points on the two retinas, for example to the fovea of each eye. By definition, the points have zero binocular disparity and will be perceived as a single fused point of light. If now the point in the right eye is moved rightwards to the limit of Panum's fusional region (assuming no eye movements), a single fused point will still be perceived. But the monocular visual direction of the point in the right eye has been changed by perhaps 10'. The question is: how will the binocular fused image change its visual direction? The answer proposed by Hering was that the binocular visual direction shifts to lie approximately halfway between the directions of the monocular images.

Subsequently, investigators such as Verhoeff (1902), Fry (1950) and Ogle (1958) generally upheld this conclusion, but reported a good deal of variability in the percepts both for a given observer and between observers. This may have been partly due to a lack of control of vergence eye movements. The definitive study on this topic is that of Sheedy and Fry (1979), who used a stimulus with a complex binocular surround, which effectively allowed the observers to hold vergence at a fixed value. They also used a stimulus line with a vertical disparity, in order to study the fusion system without contamination by the stereoscopic system. Under these conditions the position of the binocular image, averaged over observers, was almost exactly halfway between the two monocular positions. However, each observer had a stable idiosyncratic position that was closer to one monocular position than the other.

**Corresponding Retinal Points**

The perceived relative distances of objects from the observer are determined in general by the binocular disparity between the images falling on the retinae of the two eyes (in conjunction with the convergence of the eyes). Binocular disparity is defined as the angular distance from a position of correspondence in the two eyes. Corresponding points are, therefore, points having zero binocular disparity on the two retinae. The simplest definition is based on ocular geometry (Fig. 2.1), in which corresponding points on the two retinae are defined as being at the same visual direction, i.e. the same angular distance both horizontally and vertically from the centre of the fovea of each eye. These angular distances may be measured by the monocular visual directions of the stimuli in each eye (assuming no ocular torsion).

For every position of binocular fixation, there must be a set of points in space which project with zero binocular disparity onto the retinae. The locus of points in space which have zero binocular disparity is known as the horopter (the horizon of vision), a term introduced by Aguinonius (1613). The point horopter is the locus of zero disparities for point stimuli (i.e. where both horizontal and vertical disparities are zero). Ideally, the point horopter is a horizontal circle and a vertical line intersecting at the point of fixation, although in certain restricted circumstances it may become a two-dimensional surface. Under no circumstances is the point horopter ever a sphere or a torus, as has mistakenly been claimed by some authors.

**Types of Horopter**

There has been considerable confusion in the literature due to laxity in the definition of the horopter. Walls (1952), for example, maintained that there is only one horopter, with many ways of measuring it. This is incorrect. The form of the horopter depends in principle upon its definition. The definition may be based upon zero binocular disparity, zero horizontal disparity, equal perceived distance from the observer, etc. In each case the analytic form of the horopter is different, as a result of the different geometries involved in the definition. The equidistance horopter, for example, should be a sphere with its centre between the eyes, while the horizontal circle of the point horopter (just described) itself passes through the eyes with its centre in front of the observer, halfway between the eyes and the point of regard.

The horopter based on solely horizontal disparities is especially interesting because it is these disparities that are involved in depth perception. This is equivalent to a horopter measured with long vertical lines, and is therefore known as the longitudinal horopter by analogy with the
vertical lines of longitude on the globe of the earth. The longitudinal (or vertical line) horopter is the one most commonly specified in texts, and most often measured empirically. It is important to note that, as distinct from the point horopter, the line horopter is always a two-dimensional surface. The form of the surface depends on the orientation of the lines selected to define the horopter. The point horopter, on the other hand, is never a surface (except for fixation at infinity). For all other cases the point horopter is only an intersecting curve and line, and does not exist in any other directions. The details of the form of the point horopter form the bulk of the following sections.

The definition of the horopters used thus far has been purely geometric. These geometric horopters must be distinguished from the empirical horopters measured on a given observer, which may be found to deviate from the particular geometric construction implied by the measurement operation. Such an empirical deviation from the geometric prediction may occur either if physiological correspondence departs from the geometric definition of corresponding points, or if there are optical distortions of the images.

A further type of empirical horopter is based on the range of binocular fusion, and is the locus of points in space which appear binocularly fused to the observer. The fusion horopter is defined in terms of fusion of both horizontal and vertical disparities, and is therefore a three-dimensional volume in space extending around the point horopter. However, its quantitative volume has a physiological rather than a geometric basis. It is the horopter most relevant to ophthalmologic and optometric practice.

A second example of a purely empirical horopter is the stereacuity horopter. This is the locus of points which are indiscernible from zero disparity. It is defined solely in terms of horizontal disparity, and is therefore a volume of space (or slab) around the longitudinal horopter surface.

Finally, to extend the horopter concept to perception of objects in space, it is possible to base the definition on distance from the observer, rather than on binocular disparity per se. The perception of distance from the self involves activity at a higher level of the perceptual apparatus, which may add compensations, distortions and plasticity relative to the invariant form of the binocular correspondence horopter. The perceived distance horopter is therefore not as fundamental a concept as the binocular correspondence horopter. Two procedures have been used to measure the distance horopter. In one procedure, stimuli in different directions are set to appear equidistant. This establishes the equidistance horopter. In the other procedure stimuli are set to form an apparent fronto-parallel plane. This defines the fronto-parallel horopter. A fuller description of these types of distance horopter is beyond the scope of this chapter, but may be found in Ogle (1962).

Significance of the Point Horopter and the Role of Vertical Disparities

Much of the literature since the time of Helmholtz and Hering has concentrated on the longitudinal horopter, which ignores the influence of vertical disparities, and has avoided the analysis of the point horopter. While it is true that vertical disparity does not give rise to depth perception directly (Hering, 1864; Ogle, 1955), the presence of vertical disparity at a point will degrade the perception of depth from horizontal disparities at that point. Ogle (1955), studying stereocuity at 0.5° above the fovea, found that the degradation appeared to be a continuous function of the vertical disparity, and began to be detectable at a vertical disparity of about 1°. A similar conclusion was reached by Friedman et al. (1978). Mitchell (1970) found that horizontal vergence eye movements were attenuated by the presence of vertical disparities of up to 1°, depending on the stimulus configuration. Thus for both depth perception and vergence eye movements the presence of vertical disparities has a substantial (if negative) effect on disparity processing.

Vertical disparities are also of direct relevance to the fusion system, since their presence can cause diplopia even more readily than do horizontal disparities. A study by Schor and Tyler (1981), for example, shows that vertical disparities as small as 1° may be out of the fusional range for some types of stimuli, such as those involving fine detail moving at a rapid rate.

It follows that a description of the metric of binocular space in terms of horizontal disparities alone is incomplete, and that the longitudinal criterion for the definition of the horopter is insufficient. For this reason an extensive description of the neglected point horopter, which takes vertical disparity fully into account, is provided in the following sections. It has even been suggested that the resultant vertical disparities may be used by the visual system as a cue to the angle of convergence onto the fixation point (Helmholtz, 1866) and to the direction in which the eyes are pointing (Householder, 1943). The sensory effects of vertical disparity are reviewed in more detail in a subsequent section.

Vector Representation of the Point Horopter

A graphic representation of the horopter geometry may be obtained from a vector plot of the disparity fields produced by particular objects in space. The object corres-
Fig. 2.2 Projection geometry for the fronto-parallel plane. (a) Each eye views a fronto-parallel grid plane from a slight angle, inducing opposite perspective distortions in the left (L) and right (R) images. The resultant disparities give rise to the form of the correspondence horopter. (b) Horizontal and vertical disparities at many points on the grid are combined into the vector angles and magnitudes. The field of geometric disparities is for a flat plane viewed at 20 cm and slightly in front of the fixation point. Field size is ±35° in each direction. Note the vertical component to all the disparities except on the vertical and horizontal meridians.

When the binocular relationships between the monocular images are considered, a set of vectors may be derived with the tail at each point in one eye's image and the head at the equivalent point of the right eye's image (Fig. 2.2(b)). This disparity vector field encapsulates the disparity relationships over the entire binocular domain. For all points where the disparity vectors have zero length the point horopter falls at the location of the object in space. For all points with only horizontal (uncrossed) disparity there is some real distance at which the horopter may be found along the same line of sight. The same is true of points with only horizontal crossed disparity, up to the angle of convergence. In both cases, the existing horizontal disparity may be cancelled by moving the point along the line of sight in depth, ultimately resulting in a zero disparity.

Conversely, it may be stated unequivocally that all points with any vertical component to the disparity vector can never lie on the point horopter for that particular eye position. Moving the point along the line of sight will vary only its horizontal disparity, leaving the vertical disparity unaffected. Note, therefore, that the perspective distortions introduced by viewing a flat plane are such as to produce vertical disparities almost everywhere. Only on the vertical midline do the disparity vectors have zero length, so this is the only line where the fixated frontal plane corresponds to the horopter. Only on the horizontal meridian are the vectors solely horizontal, so this is the only place where the distance of the plane could be modified to move it to the horopter. In fact, the required modification is to curve the plane into a cylinder passing through the two eyes, as will be seen.

Shear of the Vertical Meridians

When measuring the monocular perception of vertical, Volkmann (1839) and Helmholtz (1866) found that corresponding meridians in the vertical direction are each tilted outwards about 1° from the true vertical, even when the eyes are in the primary gaze position. No such tilt of corresponding meridians appears in the horizontal direction, as would be expected if the tilt resulted from a relative rotation between the two monocular images. Because tilt is limited to the vertical direction, it is best described as a shear of retinal correspondence. Strictly speaking, it is an empirical deviation from the geometric form of the horopter, but it is included in the geometric analysis with the justification that the shear has many profound geometrical implications which are best developed concurrently with the true geometry.

Only recently have any direct measurements of binocular correspondence in the vertical meridian have been attempted. Measurements over a 60° range using a method of minimal interocular apparent movement were reported by Nakayama et al. (1977) and Nakayama (1977), in both the horizontal and vertical meridians. The data for four observers are shown in Fig. 2.3.

A major requirement is to establish whether there is any cyclovergence between the two eyes. This was achieved by measuring vertical disparities for stimuli with the horizontal meridians (lower graphs in Fig. 2.3). It can be seen that there is very little systematic deviation in this meridian, so that cyclovergence is less than 1° for any observer. For
Fig. 2.3 Measurements of the tilt of the vertical horopter by nulling the visual direction of interocular apparent motion, for four observers. Upper graphs of each pair show horizontal disparities as a function of distance up and down the vertical meridian. Lower graphs in each pair are control data for ocular cycloversion, showing vertical disparities along the horizontal meridian. Reproduced with permission (Nakayama, 1977).
horizontal disparities with stimuli in the vertical meridian, on the other hand, a substantial deviation from the geometrical zero line is evident (upper graphs in Fig. 2.3). This corresponds to an interocular tilt between the corresponding vertical meridians of between 2°–5°.

The data essentially confirm Helmholtz’ analysis in three interesting particulars:

1. There is a relative extorsion of the corresponding vertical meridians of the two retinas which has substantial implications for the form of the horopter away from the median plane.

2. This extorsion is not due to cyclorotation or optical factors, but must be attributed to a shear in the cortical representation of the retinal projections from the two eyes.

3. The data are a good fit to a straight line, confirming that the empirical vertical horopter is a straight (inclined) line in space and does not form a toroid or any other curved surface, as has sometimes been supposed in the past.

The tilt of the vertical horopter provides a nice explanation for some results of Breitmeyer et al. (1976), who set out to do stereoperimetry in the foveal region using dynamic random-dot stereograms with a 6° stereoscopic test field. They found an up-down anisotropy such that in the upper field best detection was behind the point of fixation, while in the lower field it was in front of the point of fixation. The regions of best detection correspond well with the points at which the stereoscopic plane formed by the random dots projects onto the inclined vertical horopter, although the authors made no reference to Helmholtz’ analysis at the time.

The Point Horopter

Fixation at Infinity and the Helmholtz Vertical Shear

The simplest case of all for the point horopter is when fixation is at optical infinity. Here rays from each point in the frontal plane at infinity are parallel and this is therefore the only case where the geometric point horopter can be considered a plane, rather than a one-dimensional configuration of lines in space.

The Helmholtz shear of the vertical meridians has a profound effect on the plane of the point horopter for parallel fixation. Fig. 2.4(a) shows the projection through the pupil of the corresponding vertical meridian of each eye, when convergence is parallel and symmetrical. Each projection forms a plane in space, and the intersection of these two planes defines the vertical horopter for the vertical meridians, which is inclined backwards in space. If the relative tilt or shear of the corresponding vertical meridians is fixed, it follows that the inclination of the vertical horopter varies with fixation distance (Fig. 2.4(b)). For fixation at infinity, the projected planes meet in a horizontal line running below the eyes, roughly in the plane of the ground when the observer is standing. For parallel fixation on the horizon the projections of all other meridians corresponding points will also intersect in the ground plane extending to the horizon. Helmholtz therefore suggested that the 2° shear has an adaptive function of bringing the horopter into the plane of the ground, upon which are located most of the objects that are of survival value to the human organism.

The Point Horopter with Symmetrical Fixation in the Visual Plane

To introduce the basic form of the point horopter, a simplified case will be considered with only symmetrical 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.

Allowing symmetrical convergence at points closer to the observer than infinity has another consequence of significance concerning points away from the horizontal or vertical axes. This case will be analysed on the assumption that no cyclorotatory eye movements occur. As shown in Figs. 2.3 and 2.5, it is generally the case that off-axis points in space project to the two retinas with both horizontal and vertical disparities. With convergence, the only exceptions occur when a point is at the distance corresponding to the horopter, which would nullify the horizontal disparity. But note that nothing can be done to nullify the vertical disparity consequent on the fact that off-axis points are necessarily closer to one eye than the other, with a resulting difference in magnification of the vertical projection angle in the two eyes. Thus, all off-axis points in a frontal plane through the fixation point project with some vertical disparity to the two eyes, and are therefore not included in the horopter (unless fixation is at infinity).

The only points in space that will project in correspondence, in this case, are those in the vertical midline as described in the previous section, and those along the horizontal midline through the fovea. The latter form a component of the symmetrical point horopter usually called the Vieth-Muller circle (though it was first specified by Agulonius, 1613). The Vieth-Muller circle passes horizontally through the point of fixation and the nodal points of the two eyes, since in this circle all points on the circumference have the same binocular disparity. It should be emphasized that all other points in space project with some horizontal and/or vertical disparity to the two eyes, and are therefore not part of the point horopter. The geometric point horopter for symmetrical fixation in the
horizontal visual plane, therefore, consists solely of a vertical line inclined backwards and a horizontal circle (dashed lines in Fig. 2.5).

**Effect of Asymmetrical Fixation within the Visual Plane**

In asymmetrical fixation the point of convergence lies to the left or to the right of the straight-ahead position. Asymmetrical convergence is an important case to consider, not only because it occurs in normal viewing, but also because in many respects it is equivalent to symmetrical fixation with a unilateral image magnification (aniseikonia), such as occurs in unilateral aphakia (lens removal). The left and right retinal images are different sizes in asymmetrical convergence because the viewed object is necessarily closer to one eye than the other. The simplest type of asymmetrical convergence is where the point of convergence lies in a horizontal plane passing through the eyes. Here the same logic of equal angles that generated the Vieth-Muller circle implies that as the eyes fixate at different points around a given Vieth-Muller circle, the angle of convergence remains constant. Thus, all non-fixated points on the circle remain in correspondence, and the horizontal horopter component always falls on the same circle.

Furthermore, the vertical line component of the horopter also remains essentially fixed in space directly in front of the observer as the eyes are moved around the Vieth-Muller circle, rather than following the position of the fixation (Fig. 2.6(a)). This occurs because the difference in image magnification away from the vertical meridian is a function of the distance of the image from each eye, which is essentially unaffected by ocular rotation (except to the extent that the centre of rotation differs slightly from the nodal point of the eye). The only position where the magnification remains equal is straight-ahead, so this remains on the horopter (which projects onto peripheral loci on the retinæ).
Thus, in eccentric fixation to the right the foveal image in the right eye is magnified relative to that in the left eye, even at the fovea. The immediate consequence of this geometry is that in eccentric fixation, regions projecting immediately above and below the fovea have an inherent vertical disparity which interdicts them from the horopter. It would seem that the presence of this vertical disparity must affect both stereopsis and fusion, but this prediction does not seem to have been subjected to experimental evaluation.

The Generalized Point Horopter

Finally, the most general case is to allow fixation at any point, involving asymmetrical convergence away from both the median and horizontal planes. This case was developed in detail by Helmholtz (1866) and is a curve of the third degree which forms a single loop spiral (Fig. 2.6(b)) within an abstract cylinder projected up and down from the Vieth-Muller circle. For any point of generalized asymmetrical fixation, the point horopter consists solely of this single loop spiral line.

Helmholtz' curve may be construed as the geometric result of stretching the line and circle horopter away from the straight ahead position so as to pass instead through the point of asymmetrical 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 infinity.

It is evident from this analysis that the ocular geometry of two eyes in asymmetric convergence produces a complex pattern of vertical disparities throughout the visual field. This pattern varies with the particular fixation direction, and also with fixation distance. At one extreme, no vertical disparities are present with fixation of a field of objects at infinity, whatever the fixation direction. However, the vertical disparities at any given eccentricity from the fixation point increase progressively as fixation is brought closer to the observer. This change in the vertical disparity field was thought by Helmholtz (1866) to be used by the visual system to gauge fixation distance.

A further prediction from the presence of vertical disparities is that, in principle, they provide information as to the eccentricity of lateral fixation (Householder, 1943; Longuet-Higgins and Mayhew, 1982; Gillam and Lawergren, 1983). The magnification of one eye's image relative to the other as a function of distance from the observer in two dimensions of space are shown in Fig. 2.7. The form in which this information occurs led these authors to propose that the artificial introduction of vertical disparities would result in the misperception of the direction of lateral fixation. The observer would then attribute to a stimulus an inappropriate horizontal depth tilt because the Vieth-Muller circle is tilted relative to the line of sight at eccentric fixation angles. This therefore constitutes an explanation for the induced effect of Ogle (1950), in which introduction of purely vertical disparities by vertical magnification of the image in one eye had the paradoxical effect of inducing a horizontal depth tilt.

These analyses are all theoretical, and little empirical work has been done to validate the physiological role of vertical disparities in human space perception. Helmholtz (1866) provided some demonstrations that vertical disparities could affect the perceived depth curvature of stimuli having zero horizontal disparity. These are precursors of Ogle's induced effect. However, in images containing oblique lines the induced effect is subject to the purely geometric explanation of horizontal disparity introduced by the rotation of the lines with a vertical magnification (Westheimer, 1978, Arditi et al., 1981). This explanation can be generalized to the oblique energy present in any 2D figure, even if oblique lines are absent as such (Westheimer, 1978).

The hypothesis of sensed eye position through vertical disparities as the complete explanation of the induced effect was severely disabled by Westheimer (1978), who showed that no effect was obtained under brief, foveal presentation conditions. It was then dealt a fatal blow by
Rogers and Koenderink (1986), who showed that two opposite induced effects could coexist in the same visual image. This could not be explained by a change in a univariate parameter such as eye position.

Nevertheless, the question has not apparently been examined from the opposite perspective. It may still be the case that the presence of vertical disparities has significant effects on depth perception. At present, there is no reason to suppose that the induced effects of vertical disparities disappear just because the vertical disparity is introduced by eccentric fixation. Thus the role of vertical disparity in space perception remains pervasive, although the components attributable to stimulus configuration as opposed to eye position have not been fully elucidated.

Effects of Eye Torsion

The occurrence of eye torsion has a direct geometric effect both on the position of the horopter and on its form. Eye torsion is a concomitant of both convergence and gaze elevation angle above or below the horizon (Nakayama, 1983). The main point of interest here is that with both convergence and gaze elevation the eyes rotate in opposite directions about the visual axes (cyclovergence), consisting of either intorsion when the tops of the eyeballs move towards from each other or extorsion when they move away from each other.

A point to emphasize is that the effects of cyclovergence are different from the effects of the shear of the vertical meridians shown in Figs. 2.3 and 2.4, even though both involve rotation of the vertical meridians. In general, shear introduces no vertical disparities, while cyclovergence introduces vertical disparities at all points away from the vertical meridian, which are maximal in the horizontal meridian. Wherever there is a vertical disparity there is no point horopter. The only region where vertical disparities are zero is in an inclined line in the median plane.

In normal individuals, cyclovergence occurs under two conditions—when the eyes are converged and when the gaze is directed downwards. The extent of such cyclovergence is detailed by Nakayama (1983) but in each case reaches a maximal value of about 3°. The two effects are additive. Fig. 2.8(a) shows the effect of convergence extorsion on the point horopter with fixation at eye level before and after cyclovergence is taken into account. The vertical horopter becomes inclined with the top further away from the observer, while still passing through the fixation point. The Vieth-Muller circle becomes inclined down out of the visual plane. As before, no other points in visual space are in both horizontal and vertical correspondence.
Fig. 2.7 Variation in vertical disparity with viewing distance. Each circle shows the locus in space for each specified percentage magnification of the image in the right eye. This corresponds to the locus of constant vertical disparities for a fixed image height above or below horizontal. Reproduced with permission (Gillam and Lawergren, 1983).

Directing the gaze up or down, without altering convergence, also induces cyclovergence, generally extorsion. The most consistent effect is in down-gaze, which will be the only case discussed here. Two conditions will be considered; down-gaze with fixation at infinity and down-gaze with convergence.

Parallel down-gaze, which is unlikely for a standing observer, might occur if the observer were lying on the ground with the head raised to look at the horizon. In this situation, the eyes would extort by about 3°, conveniently causing the horopter to become horizontal in the manner described above. It will be below but parallel to the ground plane, although, as already pointed out, the fact that it is being produced by cyclovergence will constrain it to a single line rather than a plane.

Finally, extorsion accompanying down-gaze will add to that induced by convergence if fixation is brought to a near point (Fig. 2.8(a)). This is a common occurrence; it occurs, for example, when a person reads a book. It will further incline the vertical horopter in relation to its position in down-gaze if no cyclovergence were to occur. This case is illustrated in Fig. 2.8(b), with the dashed lines showing the position of the horopter without cyclovergence, and the full lines indicating its position after cyclovergence is taken into account.

Fig. 2.8 (a) Additional tilt of horopter produced by cyclovergence occurring with convergence (full lines). Inset shows frontal view of ocular torsion. Dashed lines show horopter without cyclovergence, for the same fixation position. (b) Further tilt of horopter (full line) from geometric position in down-gaze (dashed line) caused by convergent plus down-gaze extorsion.

Empirical Deviations from the Geometric Horopter

The Vieth-Muller Circle in the Visual Plane

As mentioned, measurements of the empirical longitudinal horopter by Hering (1864) and Hillebrand (1893)
showed a consistent deviation from the geometric Vieth-Muller 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. Ogle (1932, 1950) showed that the empirical horopter in the visual plane is well described by a curve from the mathematical class of conic sections, which would imply that it is either a circle, ellipse, straight line or hyperbola, depending on the radius of curvature at the point of fixation. When there is no deviation from the Vieth-Muller circle that the horopter will remain a circle with varying radius as fixation distance is changed.

One simple hypothesis for the Hering-Hillebrand deviation from the Vieth-Muller circle is that the deviation is the result of a fixed additional angular disparity at each angle of eccentricity. In this case, the analytic form of the horopter will change with fixation distance. A family of curves for different fixation distances is shown in Fig. 2.9,

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**Fig. 2.9** Hering-Hillebrand deviation (points and dashed lines) from the geometric horopter circle (full line arcs). Note the change in form of the deviation with fixation distance, although the retinal disparity maintains a fixed deviation from geometrical correspondence. Reproduced with permission (Ogle, 1950).

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illustrating how the empirical horopter progressively curves away from the observer as fixation distance increases.

The fact that the shape of the horopter varies with fixation distance has been taken as evidence for plasticity in correspondence with changes in vergence angle (Ogle, 1962). It is therefore important to emphasize that in angular terms the Hering-Hillebrand deviation does appear to remain fixed while fixation distance is varied. This should be expected if there were a fixed, non-plastic deviation from geometric correspondence, as was originally proposed by Hillebrand (1893).

The form of the Hering-Hillebrand deviation is as expected if the nasal eccentricity is larger than the temporal eccentricity for every pair of corresponding points, and if this difference increases with eccentricity. Thus a point in the left visual field must project at a great distance on nasal retina of the left eye than on the temporal retina of the right eye, in order to hit corresponding receptors. Hence the point must lie behind the geometric Vieth-Muller circle. If this non-congruence of corresponding retinal points is fixed, it would be equivalent to a constant angular deviation of the empirical horopter from the Vieth-Muller circle, as the empirical horopter varies its curvature with fixation distance.

**Effects of the Vertical Horopter Inclination**

The backward inclination of the vertical horopter already described is a second deviation from the true geometric horopter. This raises the question of what effect it might have on the perception of vertical lines. This question was addressed by Breitmeyer et al. (1977), who found a marginally significant forward inclination of perceived vertical, but their interpretation in terms of disparity space was indecipherable. A more rigorous approach was taken by Cogan (1979), who made a direct comparison between horopter inclination and perceived inclination in depth. He first confirmed in a dichoptic task that the observers showed a relative shear of the monocular vertical meridians (between 1.5–3.2° for his eight observers). At the viewing distance of 1 m these monocular tilts correspond to a mean inclination in space of 31° (top of line tilting backwards). He then asked observers to set a binocularly viewed line to appear vertical. On average, they inclined the line only 3° backwards. Thus perceived vertical was almost vertical, and perceptual compensation for the 31° backward inclination of the vertical horopter was almost complete.

Another phenomenon which can be explained by the inclination of the vertical horopter is the break-up of vertical gratings into a series of strips in different depth planes. These have been described as binocular moire fringes when observed in vertical gratings (Piggins, 1978). Such fringes are best observed in gratings modulating in counterphase, and seem to occur because, at each height, the perceived depth of the grating is given by the disparity of the cycle closest to the position of the vertical horopter (Tyler, 1980). Thus the closest disparity will remain at the disparity of one grating cycle until the next cycle reaches the level of being the closest disparity, when
the perceived depth will jump one full cycle to this new disparity. This and the above result exemplify the way in which the rather abstract construct of the vertical horopter can influence the perception of diverse stimuli.

Ecological Significance of the Vertical Horopter Inclination

It has already been mentioned that the average shear of the vertical meridians of about 2° in humans happens to place the horopter in the ground plane when fixating at infinity. The ecological significance of this observation was commented upon by Helmholtz himself. He found himself stumbling when he attempted to walk along a mountain path without his spectacles, and attributed this to a shift of his horopter up to knee level caused by the optical aberrations (uncorrected astigmatism).

The functional role of the horopter inclination was subjected to more rigorous study in several species by Cooper and Pettigrew (1979). They first measured the anatomical position of the vertical meridian by retrograde transmission of horseradish peroxidase from the optic nerve after decussation. They had observed that the anaesthesia used in typical animal experimentation caused encycloergence (opposite rotation outward) of the vertical meridians, and therefore took care to mark the torsional positions of the globes prior to anaesthesia. They were thus able to measure the physiological tilt of the vertical meridians directly in three species (two owls and the cat).

In cat, the angle between the vertical meridians was found to be about 20°. Although much larger than the value in humans, this was just about the value required to bring the vertical horopter for distant fixation into the ground plane at a height of 10 cm in this species. A similar geometry pertained to a species of burrowing owl, which spent most of its time on the ground. Conversely, a second species of owl which rarely perched on the ground, but spent most of its time in tall trees, was found to have essentially zero tilt between the vertical meridians. Including the human result, this amounts to four different species in which the horopter angle closely matched the wide-ranging ecological requirements of the ground plane. This remarkable correspondence suggests that there may be some mechanism by which the horopter becomes aligned to the predominant environmental surfaces.

Krekling and Blika (1983) have made the further suggestion that the environmental requirements change by about a factor of two during development, and that the disparity distribution for binocular cells may exhibit sufficient plasticity to follow such a change. It should be noted that, although their calculation took into account the development of both height and interocular distance, it did not consider changes in posture. Infants up to about one year rarely stand, but spend most of their active time lying on the floor or crawling. They might therefore be expected to develop a horopter tilt corresponding to a height of about 10–20 cm above the ground, as opposed to the 60 cm expected on the basis of their body height. Since human infants develop excellent stereopsis by about four months of age (Birch et al., 1982), it is not inconceivable that such development of the horopter inclination might be measurable in human infants.

Characteristics of Fusion

As mentioned in the introduction, disparate stimuli appear fused for normally-sighted subjects up to a particular disparity value, beyond which they give rise to diplopia (double vision), in which both monocular stimuli are seen simultaneously. Historically, the ability to form a single, fused image from two separate monocular images in different positions has excited much interest and controversy. The recent growth in understanding of the cellular basis of cortical binocularity provides a much firmer basis for the understanding of the fusion process.

Physiological Basis of Fusion and Diplopia

An appropriate resolution of the controversy over fusion arises from consideration of the physiological basis of binocularity in the visual cortex, as suggested by Tyler (1983). An initial version of the physiological hypothesis was based on the distribution of disparities of the binocular receptive fields (Joshua and Bishop, 1970). In its current form this hypothesis would rely on neurophysiological data on different types of binocular neurones in the visual cortex. Hubel and Wiesel (1962) showed that some neurones in cat cortex could be driven by stimulation of an appropriate region of either eye (binocular neurones), whereas others showed an excitatory response only to stimulation of one eye (which I will term monovalent neurones, to avoid specification in terms of the inhibitory interactions). Barlow et al. (1967) and Hubel and Wiesel (1970) have found that while some binocular neurones had receptive fields at exactly corresponding points on the two retinæ, others had receptive fields with various degrees of binocular disparity in one of any of the retinal meridians. The monovalent neurones were first thought to have solely monocular responses, but are now known to have more complex binocular properties. In fact, many show inhibition to stimulation in the other eye over a large range of disparities (usually either crossed or uncrossed, but not both).

Thus, neurophysiologically we may define four classes
of neurones having excitatory receptive fields of the form: binocular corresponding, binocular disparate, monocular right and monocular left receptive fields (Fig. 2.10). Presumably, each neurone is labelled in some way as deriving stimulation from a specific visual direction. The visual direction for the excitatory receptive field is unambiguous for all classes except the binocular disparate, for which the visual direction will be assumed to fall midway between the two monocular receptive field directions for that neurone.

When static stimuli are presented to corresponding retinal points, the binocular corresponding neurones and monovalent right and left neurones with the same local sign will be stimulated. Since all three types have the same visual direction label, there is no conflict and the stimulus, encoded as the sum of all neurones responding, is seen as single. If other conditions pertain to inhibit the monovalent neurone responses (such as moving stimuli; Cynader and Regan, 1978), then equally there is no conflict with the visual direction of the binocular neurones.

When a small disparity is introduced between the points, some binocular disparate neurones are stimulated and the binocular corresponding neurones should cease responding (after an initial transient response to the disparity change; Poggio et al., 1988). But now the monovalent right and monovalent left neurones which receive equivalent images have local signs slightly to either side of the mean visual direction signalled by the binocular disparate neurones (Fig. 2.10). It is assumed that the two monocular visual directions, which would be discriminably different if presented singly, are integrated with that signalled by the binocular disparate neurones. There should, therefore, be a range of small disparities which then gives a unitary perception of a fused stimulus.

Finally, if the disparity between the two points is increased beyond the range in which the binocular responses can be integrated with the two monocular excitatory responses, each monocular response is associated with a different visual direction and two diplopic sets of stimuli are perceived. Thus, the neurophysiological results can explain many perceptual states arising from binocular stimulation. Note, however, that the basic disparity in binocular receptive fields has been considered as a basis for fusion and departures from it. The functions of stereopsis may require more complex mechanisms (Pettigrew et al., 1968; Poggio and Fischer, 1977; Tyler, 1983).

Retinal Eccentricity, Fusion and Cyclofusion

The limiting disparity at which binocular fusion breaks down varies as a function of retinal eccentricity (Fig. 2.11a), (an average of the three observers fully measured by Ogle, 1950). Thus, Panum's area is not a fixed size, but increases roughly in proportion to distance from the fovea. This increase in fusion limit is adaptive from three standpoints. One is that the size of retinal receptive fields and, hence, visual acuity both show a 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 each point.

The increase in Panum's area is also adaptive in terms of the binocular environment. Fig. 2.11(b) showed the disparities produced by binocular viewing of a plane parallel the vertical horopter at a distance of 50 cm. The disparities of points lying in the plane at large distances from the foveae are substantial, and increase roughly in proportion to degree of eccentricity. A corresponding increase in Panum's area, therefore, allows a much larger region of such a plane to appear fused than would otherwise be the case. Note
Fig. 2.11 (a) Variation in the horizontal disparity of Panum's area of binocular fusion with retinal eccentricity (the average of three observers measured by Ogle, 1950). (b) Array of disparity vectors for a flat plane aligned with the horopter, as a function of height and eccentricity in the visual field.

Fig. 2.12 (a) The empirical fusion horopter for symmetric fixation in the visual plane. Note the spread away from the geometric horopter (dashed line) due to the Helmholtz shear of the vertical meridians. (b) The generalized empirical fusion horopter for any other fixation point. Note that asymmetric fixation produces a dramatic reduction of the fused region near the fixation point.

that, if the vertical horopter is inclined in space (as shown in Figs. 2.3 and 2.4) then the disparities in Fig. 2.11(b) occur relative to that plane. Any other plane will project with even greater disparities than those depicted. Thus, the optimal angle to view any planar object is such that its plane would pass about 5 ft below the eyes (through the feet when standing). This backward inclination thus depends on viewing distance, and is the angle to adopt for maximum comfort when viewing computer and display screens.

The third reason why it is helpful to have fusion increasing with eccentricity is that it allows a degree of sensory cyclofuson. If Panum's area remained constant at all eccentricities, then the maximum cyclodisparity between two lines extending across the retinas would remain fused and would be only about 4°. As it is, the increase in Panum's area with eccentricity theoretically allows fusion for up to about 2° of cyclodisparity (Ogle, 1950). In practice, the extent of cyclofuson depends on the size and configuration of the stimulus (Kertesz, Chap-
The Fusion Horopter

One can determine the total region of space around a given point of convergence for which point stimuli appear fused. This empirical fusion horopter is depicted in Fig. 2.12(a) for the special case of symmetric convergence in the visual plane. Note that the fusion horopter runs wide of the geometric Vieth-Müller circle due to the Hering-Hillebrand deviation. The tubular form of the fusion volume is derived from the interplay between the increasing disparities that are accepted as fused with eccentricity, and the increased amount of vertical disparity that places more fusional demand on the system with the distance from fixation. Quantification of both parameters requires explicit knowledge of the precise stimulus conditions, since fusion varies dramatically with the size, orientation, luminance, velocity, etc. of the stimuli under observation (see following sections).

Fig. 2.12(b) illustrates the general case of asymmetric convergence off the visual plane, based on the Helmholtz one-turn helix described in a previous section. The narrowing of Panum’s area near fixation (Fig. 2.11a) now produces thinning of the asymmetric fusion horopter around the line of sight. But the narrowest range of fusion no longer occurs in primary position, where the fusional demand is the smallest. It is moved to an eccentric fixation direction where the vertical disparities increased rapidly with distance from the fixation point, producing a pronounced constriction of the fusional volume near fixation. The strange forms in Fig. 2.12 represent the only regions of space which produce fused visual images of point sources of light under the selected conditions of fixation. Linksz (1954) suggested that the fusion horopter has the form of a torus, but his analysis is both geometrically and empirically incorrect.

The Spatial Limits of Fusion

It is the common experience that larger objects in the field remain fused over a greater range of disparities than smaller objects. To this extent, fusion depends on the spatial extent of the stimulus. It is also unsurprising that blurred images will show a greater fusional range than sharply-focussed images. This effect was quantified by Schor et al. (1984), who compared the fusional range for bars with sharp edges and for bars with a Difference-of-Gaussian (DoG) luminance profile. The latter are closely related to blurred bars, and showed progressively increasing fusion limits as bar width was increased. The sharp-

edged bars, by contrast, showed almost no dependence of the fusion range on bar width. Thus the fusion limit is not affected by size per se, but by some aspect of the spatial frequency content of their image. In the case of the DoG profiles, varying the size concomitantly scaled the distribution of spatial frequencies in the stimuli to be fused.

The pronounced variation of fusion limits with the size of blurred images raises the question of the primitive feature controlling the behaviour of the fusion limit. As the DoG profiles become wider, the luminance gradient on each side becomes shallower. The increased fusional range might therefore be attributable either to the shallower luminance gradient or to the inherent width of the DoG profile. This issue can be decided by varying the luminance gradient without changing the width. Schor et al. (1989) used two methods to dissociate these possibilities; varying the contrast of the profile, and varying the phases of frequency components making up the luminance profiles. As depicted in Fig. 2.13, variation of contrast

![Fig. 2.13 Constancy of fusion limits over a wide range of stimulus contrasts. The stimuli were vertical bars with difference-of-Gaussian luminance profiles. For the upper graph, the disparity at which the bars just began to appear disparate was measured for two bar widths (specified in terms of the mean spatial frequency in the profile). The lower graph shows additional fusion measurements for vertical disparities in horizontal bar stimuli. In no case did bar contrast have any detectable effect upon fusion range.](image-url)
between 5 and 80% had no detectable effect on the fusional range, for either narrow or wide luminance profiles, or for either horizontal or vertical disparities.

Moreover, the same authors used several methods of manipulating the relative phases of the spatial frequency components making up fusion targets so as to maximize the differences in luminance gradient. Thus one target of a pair would be arranged to have the minimum luminance gradient, while for the other the same components would be shifted in phase so as to maximize the luminance gradients without altering their relative amplitudes. In no case did such a phase manipulation have any detectable effect on the fusion limit (Schor et al., 1989). Taken together, these results imply that the binocular fusion mechanism is completely insensitive to both the amplitude (or contrast) and the phase relations between the frequency components of the image. The only perceptual primitive important for fusion, therefore, seems to be the actual frequency content of the features. For combinations of frequency components, the fusion limit of the highest frequency component is the controlling factor.

For further exploration of the effects of spatial configuration of the retinal image, binocular fusion has been studied as a function of size of the waves in a sinusoidal line stimulus (Tyler, 1973). A sinusoidal wavy line was presented to one eye to be fused with a straight line in the other. The lines were always sharp, so if the fusion limits were controlled by the luminance profile, they should have remained constant for all configurations of the lines. When the lines were horizontal, the threshold for fusion of vertical disparities remained reasonably constant (Fig. 2.14(b)), but when they were vertical, Panum’s area for horizontal disparities varied dramatically with the size of the waves. The maximum horizontal disparity could be as much as 1° when the waves had a period of 30” per cycle, and became as small as 2’ when the period was reduced to 20” per cycle (Fig. 2.14(a)).

Note that the 30-fold variation in fusion limits all occurred with the stimulus passing through the fovea. A significant distinction must be made here between a ceiling limit such as the fusion range depicted here and a floor limit such as stereothreshold. In the case of a floor limit, threshold for a long stimulus requires that the response (in this case depth perception) is below threshold at all points along the stimulus. Detection occurs if any region exceeds the criterion level, and different retinal regions of the stimulus could mediate detection under different stimulation conditions. By contrast, a ceiling limit is such that all regions have to remain below threshold for it to meet criterion (in this case, be counted as fused). Thus if a stimulus passing through the fovea is described as fused, it must be fused in the fovea as well as everywhere else. Consequently, as long as the fusion limit is smaller in the fovea than all other retinal regions, the fusion range of a stimulus passing through the fovea must be determined by the foveal fusion limit (to the extent that it is independent of the stimulus in other retinal regions). It may be concluded that the 30-fold variations in fusional range are a property of particular retinal regions, rather than being a reflection of change in fusional properties across different regions.

Thus, the traditional concept of Panum’s area as a fixed property of a given retinal region must be abandoned. Instead, the fusional extent is strongly dependent on the stimulus used to measure it. Hence, the fusional horopter presented in the previous section is not a fixed range around the point horopter, and the depictions of Fig. 2.12 must be taken only as an indication of the fusional range in the real world; the range 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 binocular fusion is that it is established in a very short time. Helmholtz (1866) had experimented with fusion in stereograms illuminated by a (microsecond) electric spark. Woo (1974) examined the
effect of duration systematically and found that fusion appeared to be complete by about 30 ms. This is probably the same as the luminance integration time under his conditions, so the speed of fusion for flashed targets seems to be limited mainly by the rate of integration of luminance.

However, the extent of Panum's area is affected substantially by the temporal characteristics of the stimulus presentation. Fender and Julesz (1967), using a binocular retinal image stabilizer to control eye movements, increased the horizontal disparity in the stimulus from zero at various fixed rates. They found that for line stimuli Panum's area could be increased from the classic value of 14' to 65' of uncrossed disparity by continuously increasing disparity at a rate of 2'° s\(^{-1}\). (Note that the larger range found for random-dot stimuli was not in a fusion task but a depth perception task, and thus has no relation to the fusion mechanism.) In a follow-up study, Diner (1988) found that much of this increase could be attributed not to an extension of Panum's area, but to a shift in the mean disparity about which fusion occurred. The maximum rate of disparity change for which this shift could be obtained was 0.13'° s\(^{-1}\).

Another approach to the temporal characteristics of fusion is to use sinusoidal temporal modulation of the disparity. Schor and Tyler (1981) applied this approach using vertical lines 0.5' on either side of the fovea, which were disparity-modulated in counterphase. This display effectively controlled the consequences of eye movements, since vergent tracking of one stimulus to reduce its disparity would increase the disparity of the other. For eight observers the horizontal extent of Panum's area reached about 18' for low temporal frequencies up to 0.25 Hz, and then gradually declined with increasing frequency to about 3' by about 5 Hz (Fig. 2.15). Thus high temporal frequencies of horizontal disparity modulation appear to constrict Panum's area in a fashion similar to flashed presentations.

Vertical disparities show a different pattern of behaviour. If the whole display is rotated by 90°, the lines are now horizontal above and below the fovea and the disparities are vertical. Fig. 2.15 shows that with the same kind of disparity modulation the vertical range of Panum's area reaches only about 6' at low temporal frequencies, and falls to about the same value as the horizontal range at high temporal frequencies (3'). Thus it appears that the horizontal range of fusion is extended by low rates of modulation (stimulus velocities), while the vertical range is approximately constant. Whether the horizontal extension of fusion results from the kind of adaptive change in mean disparity found by Diner (1988) or by a symmetrical expansion of the fusional range at low rates of change of disparity was not investigated by Schor and Tyler (1981).

### Spatiotemporal Interaction in Fusion

The foregoing sections review the evidence that the size of the fusion area is strongly affected by either the spatial or temporal characteristics of the stimulus. This raises the issue of how fusion would be affected by the simultaneous variation of spatial and temporal properties of disparity. Would the temporal fusion characteristic have the same shape for any type of spatial disparity profile? Conversely, would the spatial characteristic remain similar at all temporal disparity modulation frequencies? Schor and Tyler (1981) studied such interactions between spatial and temporal disparity variations for both horizontal and vertical disparities. A line stimulus similar to that described above was used, but with simultaneous spatial and temporal modulation of disparity (Fig. 2.16). Thus each line in each eye had a sinusoidal spatial modulation which was amplitude-modulated sinusoidally in time.

The data are summarized in Fig. 2.16 for a full range of stimulus conditions. Each ellipse represents the disparity ranges of Panum's area under given conditions of spatial and temporal modulation of disparity. This figure emphasizes the large variation in size and shape of Panum's area with stimulus conditions. The main effect of spatial frequency of disparity modulation occurs at low temporal
The size and shape of Panum’s area varies with both temporal and spatial characteristics of disparity modulation. The horizontal diameter of Panum’s area varies from a maximum of 20 to a minimum of 1.5”, while the vertical diameter remains much more constant. At low temporal and spatial rates of disparity oscillation, the shape of Panum’s area is elliptical with a ratio of 2.3:1 between the horizontal and vertical extents. At high temporal rates the horizontal extent is reduced to equal the fixed vertical extent and the shape of Panum’s area becomes circular. Both the horizontal and vertical extents are reduced to 1.5” as the spatial differences in disparity are made finer.

A final observation from these data is that the effects were not separable, but embodied a nonlinear spatiotemporal interaction. Thus the combined spatial and temporal modulation effects on binocular fusion were not predictable from the effects of each separate type of disparity modulation. This nonseparability probably means that at least two mechanisms with different spatiotemporal properties of disparity processing are involved.

In summary, these data radically revise our conception of Panum’s area (in the situation of unstabilized vision with normal eye movements). Instead of a fixed fusional region there is a strong dependence of fusion on the local stimulus characteristics. Panum’s area is a dynamic entity that is continually being adapted to the prevailing features of the stimulus environment. In conjunction with the elaborate deformations of the horopter as the fixation and convergence angles are moved around in the environment, this makes the full specification of the range of fusion a complex task. Luckily for our visual sanity, however, we quickly develop the reflex to refixate and reconverge on any object whose diplopic image stimulates our attention. The diplopia is immediately abolished by this manoeuvre, with the result that most of the time we are unaware of the wealth of diplopia present in any particular view of the environment. It is only when forced to maintain a steady fixation posture that the extent of diplopia becomes evident.

References


