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1999 ELSEVIER Amsterdam • Lausanne • New York • Oxford • Shannon • Singapore • Tokyo occlusion therapy used for correcting the amblyopia. When the non-amblyopic eye is chronically patched, the amblyopic eye often shows an improved acuity but at the cost of a reduction of acuity in the patched eye. This reciprocity is characteristic of the effects of occlusion during the sensitive period which appears to extend throughout the early years of childhood. In addition to this clinical relevance, measuring procedures are finding direct application in two forms. First, these new tests can assess the status of the vision of infants suspected to be at risk for early pathology. Second, they can assess the visual consequences of therapy and be used to titrate the amounts of chronic treatments such as occlusion therapy.

10. Neuronal mechanisms

Many changes in relevant neuronal paths and nuclei occur during the infant's growth. The most obvious are changes in the anatomy of the retina, particularly in the region of the fovea, myelination of neurons in the optic nerve and elsewhere, and changes in cortex. Anatomical change in the fovea increases the density of photopigments in the cone receptors as well as their packing density thereby increasing both sensitivity and resolution. Changes in cortex, such as segregation of the ocular dominance columns, have been hypothesized to account for the onset of binocularity. Search for the neuronal correlates of visual development continues.

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See also Retina, vertebrate; Visual development; Psychophysics; Visual field; Visual pattern and form perception; Stcreopsis, binocular perception; Eye-head coordination; Oculomotor system, mechanisms; Myopia; Emmetropization; Visual motion perception; Color vision

Visual field

Hans Strasburger and Ernst Pöppel

The visual field refers to the number of degrees of visual angle during stable fixation of the eyes. Monocular measurement of the visual field by perimetry shows that the left and the right half of the visual field are not the same size. The temporal visual field, defined as extending from the vertical meridian toward the periphery, is considerably larger than the nasal visual field. Measurements along the horizontal meridian show that targets even beyond 90° eccentricity can be detected on the temporal side; the limit of light detection is 50–60° on the nasal side (Pöppel and Harvey, 1973). The upper and lower halves of the visual field appear to be equal, with the limits at approximately 50-60° eccentricity, although there are large individual differences. If the visual fields of the two eyes are superimposed as in normal vision, the binocular visual field covers more than 180° along the horizontal meridian. The most eccentric part of the temporal visual field that lies beyond the border of the nasal visual field of the other eye is called monocular crescent. Thus, binocular vision is provided only up to the border of the nasal visual field; the far periphery on the left and right side is seen monocularly.

Visual field measurements are usually done using a white test target of high contrast that is moved from the periphery toward the center of the visual field (dynamic perimetry). If, instead, light-difference threshold is measured at various positions of the visual field of one eye using a stationary target (static perimetry), local sensitivity can be determined. Under photopic adaptation conditions, the fovea centralis has the highest sensitivity. The perifoveal region is characterized by a decreasing sensitivity beginning at the fovea and ending approximately at 10° eccentricity. Beyond this, there is a plateau of constant sensitivity that extends up to approximately 35° eccentricity on the temporal side and up to 20° eccentricity on the nasal side. Beyond this plateau, sensitivity again decreases until the end of the visual field. The blind spot lies within the plateau region on the

temporal side, approximately between 14° and 18° eccentricity along the horizontal meridian (Figure 1). Under scotopic adaptation, the fovea and perifoveal region are less sensitive than more peripheral regions of the retina because of the shift from cone-dominated to rod-dominated vision. Under these conditions, the most sensitive part of the retina lies at approximately $10-20^{\circ}$ horizontal eccentricity on the temporal side. If a colored target instead of a white target is used for visual field measurement, subjects are able to detect the target as it is moved from the periphery toward the center of the visual field at greater eccentricities than those where they can identify its color.

Sensitivity is always determined after full adaptation to the background luminance has taken place. The dependence of sensitivity on background luminance is governed by Weber's law: The detectable luminance increment ΔL is, over a wide range, a constant fraction of background luminance *L*. The Weber fraction, or Weber contrast, $\Delta L/L$ is thus a suitable measure of sensitivity. Deviations from Weber's law occur at the ends of the visible range of luminances, i.e., at the absolute threshold in dark and in the high photopic range.

Although sensitivity varies throughout the visual field, apparent brightness remains constant under photopic adaptation; the percept does not get darker toward the periphery of the visual field (Pöppel and Harvey, 1973). Constancy of brightness throughout the visual field can be demonstrated by using a visual target of constant contrast that is above threshold for all eccentricities tested; it is then scaled with respect to its apparent brightness by the technique of magnitude estimation. Apparent brightness is directly related to the physical energy of the visual stimulus and not to local sensitivity of the retina. Note that this observation disproves Fechner's law as far as accounting for brightness perception throughout the visual field. Under scotopic adaptation, constancy of brightness throughout the visual field is observed only for the periphery; in order for foveal



Figure 1. Light-difference threshold ($\Delta L/L$, L: luminance) isopters for the right eye of E.P., determined with a 10-min arc target. The target was presented for 200 ms on a 0.85 millilambert (2.7 cd/m²) background. The visual field is represented in polar coordinates with the fovea at the origin. Horizontal and vertical meridians are marked at 10° intervals; the Weber contrast for the isopters is shown in the right lower quadrant. The contrast for foveal vision under these conditions (for the right eye of E.P.) is 0.1. The isopters are based on measurements along 12 meridians. The measurements along each meridian were obtained in steps of 2° visual angle from the fovea to the limits of the visual field. Note the plateau of constant light-difference threshold surrounding the foveal and perifoveal region with its pronounced extension into the temporal visual field (nasa retina).

and perifoveal targets to appear equally bright, they must have a higher contrast. For constancy of brightness, one has to assume a neuronal mechanism that compensates for the changing sensitivity of the retina as a function of eccentricity. It is still unclear where and how such a mechanism might work, although it has been suggested that it is already implemented at the retinal level.

If the two eyes are properly aligned while fixating an object, each position in binocular visual space is imaged to corresponding retinal points. In case of a misalignment, i.e., if the two visual axes are uncorrelated, a point in space is imaged to non-corresponding retinal points. Such a deviation of the visual axes may result in the experience of double images because the visual fields of the two eyes no longer coincide. Proper alignment of the eyes is necessary for stereoscopic vision; if not corrected in early childhood, misalignment may result in a loss of stereoscopic vision and the reduction of sensitivity in one eye.

Detection of stimuli is a necessary prerequisite for the performance of more complex visual functions such as form and object recognition or processing of positional information. Detection is not a sufficient condition, however, and there is currently no general way of inferring, from detection performance, in which parts of the visual field other visual functions are present. The areas in which such other functions are present are described by subfields of the visual field of detection. The visual field of form recognition extends about $\pm 40^{\circ}$ horizontally and $\pm 30^{\circ}$ vertically. With decreasing stimulus contrast the field of recognition shrinks further in size and covers an increasingly smaller part of the field of detection at same contrast. At the lowest visible contrast, recognition is confined to the foveal and perifoveal field (Strasburger and Rentschler, 1996).

The distribution of visual attention plays a further important role in all peripheral visual functions. Von Helmholtz has already reported in the late previous century that targets are better recognized when they are voluntarily attended without shifting visual fixation. When visual attention is fixed to the central field, the field of form recognition is further reduced in size; the resulting field has been termed the "form-resolving field" (Geiger et al., 1992).

How is the visual field represented in the brain? The first observation on visual field representation may already go back to Descartes who discovered that left and right and top and bottom of an object are reversed on the retina. Thus, the temporal visual field of each eye is represented on the nasal half of the retina, and the nasal visual field on the temporal retina. If one fixates an object and draws a vertical line through the fixation point, everything that is to the left of this line is represented on the nasal half of the retina of the left eye and on the temporal half of the retina of the right eye. Everything to the right of this line is represented on the nasal retina of the right eye and on the temporal retina of the left eye.

The output of retinal information processing is collected in approximately 1 million ganglion cells whose axons form the optic nerve. The optic nerve leaves the eye at the optic disk that corresponds perceptually to the blind spot in the visual field. The optic nerve is split into halves at the optic chiasm. Those axons that carry information from the nasal retina cross over to the other side of the brain and those axons coming from the temporal retina stay on the same side. The fiber bundle beyond the optic chiasm, the optic tract, contains the information that comes from the nasal retina of one eye and the temporal retina of the other. In summary, each visual half field is projected to the contralateral side of the brain and is thus represented on the same side as the corresponding (left or right) hand or other extremity.

Most of the fibers coming from the retina project to the lateral geniculate nucleus (LGN), a subcortical brain structure, located in the thalamus, with six layers each innervated by either the right or the left eye. Neurons in adjacent positions in the different layers are innervated by retinal fibers that represent corresponding retinal points of the two eyes. The representation of the retina in the LGN is retinotopic, i.e., the spatial structure of an object in visual space is preserved through the retina to the LGN, although within the optic nerve and the optic tract such retinotopy appears to be absent.

The LGN projects to the striate cortex via the optic radiation, and the visual field representation in the striate cortex (also called visual cortex, Area 17, occipital lobe, or V1) retains its retinotopy. At the striate cortex, the separate representations of the visual field in the different layers of the LGN are fused into one visual field representation by way of binocular innervation of cortical neurons. The specific retinotopic representation of the visual field in humans has been mapped with the help of brain-injured patients who had suffered total or partial lesions of the striate cortex (Teuber et al., 1960). The total loss of striate cortex within one hemisphere results in a complete homonymous hemianopia. A patient with such a condition has no vision in the temporal visual field of one eye and in the nasal visual field of the other. Often, such patients show a foveal sparing, which suggested early on that the fovea of each eye is represented in both hemispheres. Visual field defects can occur for a number of traumatic reasons and can take any form and size in the visual field.

Although the representation of the visual field at the striate cortex is retinotopic, the cortex does not devote equal neuronal space to equal visual space. The foveal and perifoveal region get much greater emphasis than the periphery, and this fact is expressed by way of the so-called magnification factor M (Daniel and Whitteridge, 1961; Talbot and Marshall, 1941). Not only is the density of receptors vastly higher in the central retina, but more neuronal machinery is also provided for the same region: retinal ganglion cells that process information from the central visual field are much more densely packed, and each ganglion cell in turn innervates, via the LGN, a roughly equal area of striate cortex. About 8 mm linear extent of cortical area corresponds to 1° of visual angle in the central fovea, and this number decreases as an inverse linear function of visual field eccentricity, being halved at about 4° eccentricity.

The striate cortex is surrounded by secondary areas that are also concerned with visual information processing. These extrastriate areas appear to be specialized for the analysis of particular categories of visual information like depth, movement, or color. The projections to higher areas seem organized into two streams: a ventral stream, leading to the temporal cortex, seems specialized to object recognition; and a dorsal stream, leading to the parietal cortex, seems specialized to the processing of spatial relationships or positional information. As one moves up this path of projections, the representation of the visual field in each of those higher areas is increasingly less retinotopic and is decreased in visual field extent.

Visual motion perception

Ellen C. Hildreth

When object surfaces move relative to an observer, a continually changing pattern of light intensity is projected onto the eye. Measurement of the movement of features in this changing image allows the observer to track objects, segment the scene into multiple surfaces, recover the three-dimensional (3D) The visual field is also mapped onto the superior colliculus. With an injury in the geniculostriatal pathway, this retinal projection usually remains intact. This is why the retinocollicular pathway, along with a number of other projections, is assumed to mediate certain visual functions in blindsight. The collicular representation of the visual field is probably also essential for the programming of saccadic eye movements. It is conceivable that a visual stimulus from the periphery of the visual field elicits directly a proper saccade on the basis of the collicular representation alone without involving the cortical representation. Thus, the superior colliculus has been considered an important link between the sensory representation of the visual field and the oculomotor system.

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See also Attention, selective visual; Blindsight, residual vision: Brightness; Color vision; Geniculate bodies, lateral; Psychophysics; Retina, vertebrate; Stereopsis, binocular perception; Visual adaptation, dark–light; Visual motion perception; Visual perception; Visual system, organization

shape and motion of objects, and recover the 3D movement of the observer through space. Models proposed for motion analysis in biological vision systems typically divide motion processing into two stages: (1) measurement of the direction and speed of movement of features in the two-dimensional (2D)