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"Visual Development, Infant"

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of very complex stimuli such as faces or hands but poorly to much simpler stimuli. There remains a large gap between the relatively simple levels of form selectivity that have so far been demonstrated in lower areas (V2 and V4) and the much more advanced levels suggested by these results in inferotemporal cortex. Progress on these and related issues should markedly improve our understanding of the neural basis of complex perceptual processes.

See also Cerebral Cortex; Vision, Extrageniculostriate; Visual Cortex; Visual Perception

Visual Development, Infant

Richard Held

The question "What can infants see" has long intrigued laymen and scientists alike. In recent decades a surge of new results in vision research has deepened the importance of the question and begun to provide answers. Knowledge of the status of infants' vision, its development, and the underlying neuronal mechanisms is gained by noninvasive procedures, with the exceptions of anatomical studies of postmortem tissue. Otherwise, our knowledge has been based upon observations aided by instruments, psychophysical studies, and electrophysiology done with scalp electrodes. Inferences about neuronal mechanisms are often guided by physiological and anatomical knowledge obtained from animal studies, in particular, those performed on primates. In addition to its scientific interest, the study of normal and abnormal visual development is of clinical importance in interpreting the deleterious effects of early pathologies of significant incidence in infants, such as strabismus, anisometropia, high refractive errors, and congenital cataract.

Optics

Since the source of visual stimulation is light focused on the retinas, clarity of the ocular media is important. The light transmitting media in infants' eyes are normally clear at birth and remain so. Their refracting power, including accommodation of the lens, appears to be adequate for the relatively low levels of resolution that are achieved in infancy (discussed below). Infants' refraction differs from that of adults in showing a higher incidence of astigmatism (estimated range between 20% and 60%) on different axes, less myopia, and a lessened accommodative range during the very early months of life.

Eye motility

The retina forms part of the eye that can move. Eye movement has numerous consequences for vision. Primary among these is the ability to foveate targets in order to resolve fine detail. In the case of a moving field of objects, the eyes of an adult pursue the target to maintain foveation but, being limited in their amplitude of rotation, they periodically jerk back in the opposite direction by means of rapid saccades (optokinetic nystagmus). The pursuit mechanism appears to be adequate soon after birth for low velocity targets but fails for higher velocities, a state of affairs which improves with age and which may reflect the development of the fovea. Curiously enough, when one eye of an infant of less than three months of age

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is exposed to such targets, pursuit is adequate for motion in the temporal to nasal direction but grossly ineffective for the opposite direction of motion. Not until the fourth month on average is this asymmetry overcome. In the case of head movements, a vestibularly activated reflex rotates the eyes in the compensatory direction so as to hold fixation. This ability appears to be present soon after birth. The combined orientations of the two eyes (vergence) determine the correspondence of the two retinal images and hence exert a limitation on stereopsis. Accurate vergence appears to develop over the first few months. Chronically inaccurate vergence of the two eyes is the condition called strabismus, some forms of which may cause amblyopia (a form of blindness) in infancy and lead to a permanent loss of binocularity.

Visual fields

Normal adults can detect stimuli at least 90 degrees off the optical axis of the eye on the temporal side and are limited on the nasal side only by the occluding effect of their noses. Newborn infants, however, have visual fields not extending more than 30 degrees from their optical axis. Moreover, they are more sensitive to stimuli on the temporal side. The extent of fields increases with age. It is not known whether these results reflect visual or attentional processes, or perhaps both.

Discrimination

The body of data on visual resolution obtained by the use of observational, psychophysical, and electrophysiological techniques is probably the most important source of information about the developing visual system of the infant. These techniques are designed to test for the detection and discrimination of stimuli. Perhaps most used is the preferential looking paradigm, which is based upon the original discovery that an infant will prefer to gaze in the direction of a region in its field of vision that is brighter, or has more edges, more motion, more solidity, more color, or more of some other property than other regions in the visual field. For example, an infant can be presented with a choice between a grating (typically one made up of alternating black and white bars of equal width) and a blank field of the same overall shape, average brightness, and color (Figure 1). When the bars are detectable, the infant will show gaze preference for them on repeated trials. The width of the bars can then be reduced in steps until the bars are no longer discriminable. The preference will have fallen

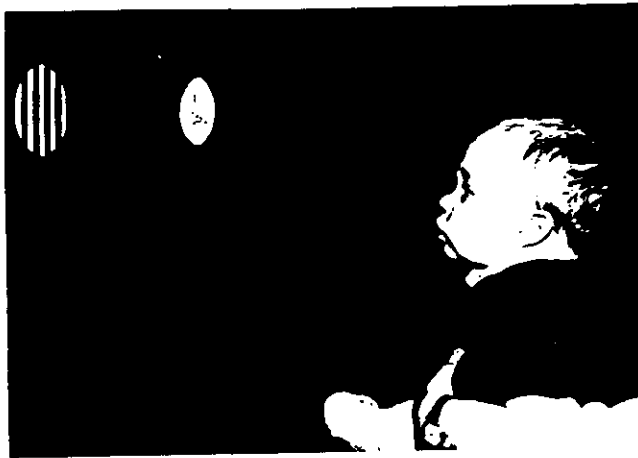


Figure 1. Preferential looking test with choice between grating and blank. Observer watches infant through peephole in screen.

to 50% (chance). The width of the bar at 75% preference is often taken as the threshold. Other properties of stimuli can be similarly varied in magnitude so as to obtain thresholds for other visual capacities.

Two types of visual capabilities can be distinguished on the basis of their developmental histories: those that are present at birth and appear to change little with age, and those that are either poor or absent at birth but improve or appear with increasing age. Among the former are brightness, color, motion, and temporal sensitivity; the latter include many forms of spatial resolution such as grating acuity, stereoacuity, and vernier acuity, several forms of binocular interaction including rivalry, binocular summation, and susceptibility to amblyopia. The latter type yield more information relevant to the underlying neuronal mechanism since they show a course of development which can be related to that of neuronal mechanisms.

Grating acuity and contrast sensitivity

The most commonly used measure of resolution is the so-called minimum separable, that is, the smallest separation in the visual angle between two edges that can be detected. The reciprocal of this measurement is referred to as visual acuity. A set of equally spaced black and white bars that form a square-wave grating is a convenient stimulus for this purpose because its spatial periodicity can easily be specified in terms of the spatial frequency (repetitions per degree of visual angle) of its components. The acuity threshold is defined as the spatial frequency of the grating which is just detectable at high contrast. The related measure of contrast sensitivity is defined as the just detectable degree of contrast at specified spatial frequencies. Contrast sensitivity across the spatial frequency spectrum can in principle determine the visibility of any achromatic form which can be harmonically analyzed into its component frequencies and their phase relations.

Using variants of the forced-choice looking preference technique, results from several laboratories agree in showing that grating acuity in newborn infants has a spatial frequency of approximately one cycle per degree of visual angle (20/600 Snellen). It increases steadily in succeeding months such that acuity in cycles per degree is roughly equal to age in months over the first year. It reaches adult levels only after 7–10 years. Tests of preterm infants have shown that this development is closely related to conceptual age, rather than postnatal

age, indicating that maturation is the important variable. The same techniques used to establish contrast sensitivity show an initial sensitivity of about one-thirtieth that of the adult level followed by a steady increase with age. The frequency of peak sensitivity increases from a fraction of a cycle to several cycles per degree over the first six months. These data are obtained by testing gratings with edges oriented either horizontally or vertically. Infants begin to show the lowered acuity for oblique relative to main axes gratings, observed in adults, by six months of age.

Amplitude measures of visually evoked potentials show initial levels of acuity roughly equal to those found by preferential looking, but the rate of increase is greater such that by six months infants show adult levels of acuity. The reasons for this discrepancy are not yet understood. On the other hand, latency measures of evoked potentials show a time course of change (reduction) similar to that of looking preference measures of acuity.

Stereopsis and binocularity

Several types of display have been used to test for stereopsis in infants. To distinguish discrimination of depth based upon stereopsis from that based upon other stimulus cues, random dot displays have been used. Alternatively, line stereograms can be used, provided that control displays demonstrate that the discrimination is, in fact, based upon stereopsis and not upon other cues to depth. Scalp potentials can be evoked by stereoptic displays. These methods yield similar results. They show an absence of stereopsis in the early months with an average onset age of four months and a range from two to six months. Additional studies show that the stereoacuity threshold rises to at least one minute of arc within a few weeks after onset of stereopsis. This abrupt rise contrasts radically with the development of grating acuity, which is present at birth and shows a relatively long slow rise with age. Since the neural signals from each of the two eyes do not converge functionally until they arrive in the visual cortex, development of that structure is suspected to underlie the onset of stereopsis and the rapid rise of stereoacuity.

Several other indices of binocularity have been developed. In the two-choice preference paradigm, stimuli which cause binocular rivalry in adult vision appear to be avoided by infants who have stereopsis. However, before the onset of stereopsis, very young infants show either no preferential response to fusible over rivalrous stimuli, or a clear preference for the rivalrous stimuli if superposition of its two views yield a figure that is more complex than the fused one. Nonselective combination of stimulus inputs to the two eyes seems to characterize vision prior to the onset of stereopsis. The transition to preference for the fused stimulus occurs at the same time as does the onset of stereopsis. Another finding which has been interpreted as an index of binocularity is the onset of binocular summation of the pupillary response. When light is available to only one eye, the pupil constricts to some constant level. When the same light is available to both eyes the pupil constricts a bit more, demonstrating binocular summation. Studies of infants show that such summation is weak in very young infants but increases to adult level by about four months of age, the same time as the onset of binocularity indices.

Vernier acuity

In adult observers the minimum separable acuity appears to have a lower limit of approximately a half minute determined by both the resolution of the optics of the eye and the grain

of the receptor mosaic. However, considerably smaller spatial differences can be detected in certain configurations. These achievements constitute the so-called hyperacuties because they exceed the limitations on the minimum separable. For example, resolution for vernier offsets (slightly displaced segments of a straight edge) as small as a few seconds of visual angle can be detected by adult observers. The study of vernier acuity in infants has revealed that vernier acuity is initially less than grating acuity but, beginning in the fourth month, exceeds it. The crossing point appears to occur at the same time as the onset of stereopsis. If hyperacuity in infants is defined as resolution significantly better than grating acuity, then the capacity for hyperacuity has its onset during the fourth month. The vernier acuity results are in accord with those from the study of hyperacute stereopsis (high stereoacuity) which also has its onset at the same age. The agreement among onset times suggests concomitant developments in the visual cortex.

Clinical relevance

During the 1960s and 1970s physiological and anatomical studies of the visual cortex in animals yielded unusually clear demonstrations of the interacting roles of maturation and exposure to the visual environment in determining the development of the visual system. Occlusion of one eye during a sensitive period early in life was shown to alter radically the central connections within cortex as well as to reduce visual function. Similar consequences were shown to follow from early strabismus. These results are relevant to analogous human pathologies such as early occlusive cataract and congenital strabismus. What is the sensitive period during which the infant may lose visual function under the conditions that are known to alter the visual nervous system? Use of new measurements of acuity has begun to reveal the onset of at least one sensitive period, i.e., the development of amblyopia resulting from esotropia (cross-eyedness in which one eye turns inward). Its earliest appearance occurs in the third or fourth month, roughly the same age as the development of binocularity. Acuity measurements have also revealed the effects of monocular occlusion therapy used for correcting the amblyopia. When the nonam-

blyopic 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.

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 may increase the packing density of receptors and hence increase resolution. Changes in cortex, such as segregation of the ocular dominance columns, may account for the onset of binocularity. The search for the neuronal correlates of visual development continues.

See also Amblyopia; Psychophysics; Stereopsis; Strabismus; Visual Field; Visual Learning; Visual System Development; Plasticity

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Visual Field

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, 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. 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. If instead light-difference threshold is measured at various positions of the visual field of one eye using a stationary target (static perimetry) in addition to visual field extent, 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

