Vision

Contributed by: Lorrin A. Riggs, Charles E. Sternheim

Publication year: 2014

The sense of sight, which perceives the form, color, size, movement, and distance of objects. Of all the senses, vision provides the most detailed and extensive information about the environment. Conversely, blindness is recognized as more disabling than deafness or any other sensory handicap. In the higher animals, especially the birds and primates, the eyes and the visual areas of the central nervous system have developed a size and complexity far beyond the other sensory systems.

Visual stimuli

These are typically rays of light entering the eyes and forming images on the retina at the back of the eyeball (**Fig. 1**). The intensity and wavelength characteristics of the light vary according to the light source and the object from which they are reflected. Human vision is most sensitive for light comprising the visible spectrum in the range 380–720 nanometers (nm) in wavelength. Sunlight and common sources of artificial light contain substantially all wavelengths in this range, but each source has a characteristic spectral energy distribution. In general, light stimuli can be measured by physical means with respect to their energy, dominant wavelength, and spectral purity. These three physical aspects of the light are closely related to the perceived brightness, hue, and saturation, respectively. *See also:* COLOR; LIGHT.

Atypical (sometimes called inadequate) stimuli for vision include momentary pressure on the eyeball, electric current through the eyes or head, a sudden blow on the back of the head, or disturbances of the central nervous system, caused by drugs, fatigue, or disease. Any of these may yield visual experiences not aroused by light. They are of interest because they show that the essentially visual character of the sensory experience is determined by the region stimulated (eyes, visual tracts) rather than by the nature of the stimulus. Indeed any observant person can detect swirling clouds or spots of “light” in total darkness or while looking at a homogeneous field such as a bright blue sky. These phenomena illustrate the spontaneous activity that is characteristic of the nervous system in general. They show that the visual system is continuously active, which in turn means that the effect of a stimulus is to modify existing activity and not merely to initiate new activity.

Anatomical basis for vision

The anatomical structures involved in vision include the eyes, optic nerves and tracts, optic thalamus, primary visual cortex, and higher visual areas of the brain. The eyes are motor organs as well as sensory; that is, each eye can turn directly toward an object to inspect it. The two eyes are coordinated in their inspection of objects, and

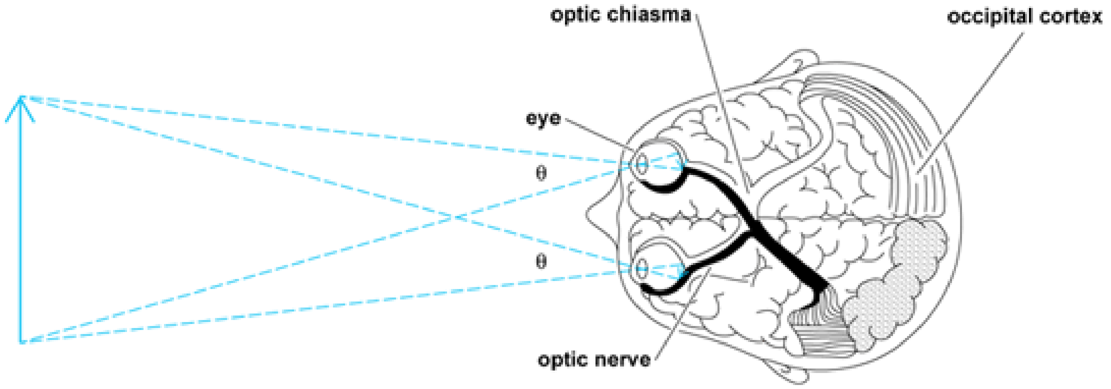

Fig. 1 **Diagram showing the eyes and visual projection system. The visual angle θ is measured in degrees.**

they are able to converge for near objects and diverge for far ones. Each eye can also regulate the shape of its crystalline lens to focus the rays from the object and to form a sharp image on the retina. Furthermore, the eyes can regulate the amount of light reaching the sensitive cells on the retina by contracting and expanding the pupil of the iris. These motor responses of the eyes are examples of involuntary action that is controlled by various reflex pathways within the brain. *See also:* EYE (VERTEBRATE).

The process of seeing begins when light passes through the eye and is absorbed by the photoreceptors of the retina. These cells are activated by the light in such a way that electrical potentials are generated. These potentials are probably responsible for many features of the electroretinogram, an electrical response wave that can be detected by means of electrodes attached to the outside of the eye. Some of these potentials are the signs of electrochemical activity that serves to generate nerve responses in various successive neural cells (bipolars, ganglion cells, and others) in the vicinity of excitation. Finally, impulses emerge from the eye in the form of repetitive discharges in the fibers of the optic nerve. It must be emphasized, however, that the optic nerve impulses do not mirror exactly the excitation of the photoreceptors by light. Complex interactions within the retina serve to enhance certain responses and to suppress others. Furthermore, it is a fact that each eye contains more than a hundred times as many photoreceptors as optic nerve fibers. Thus it would appear that much of the integrative action of the visual system has already occurred within the retina before the brain has had a chance to act.

The optic nerves from the two eyes traverse the optic chiasma. **Figure 1** shows that the fibers from the inner (nasal) half of each retina cross over to the opposite side, while those from the outer (temporal) half do not cross over but remain on the same side. The effect of this arrangement is that the right visual field, which stimulates the left half of each retina, activates the left half of the thalamus and visual cortex. Conversely the left visual field affects the right half of the brain. This situation is therefore similar to that of other sensory and motor projection systems in which the left side of the body is represented by the right side of the brain and vice versa.

Characteristics of human vision

Characteristic	Scotopic vision	Photopic vision
Photochemical substance	Rhodopsin	Cone pigments
Receptor cells	Rods	Cones
Speed of adaptation	Slow (30 min or more)	Rapid (8 min or less)
Color discrimination	No	Yes
Region of retina	Periphery	Center
Spatial summation	Much	Little
Visual acuity	Low	High
Number of receptors per eye	120,000,000	7,000,000
Cortical representation	Small	Large
Spectral sensitivity peak	505 nm	555 nm

The visual cortex includes a projection area in the occipital lobe of each hemisphere. Here there appears to be a point-for-point correspondence between the retina of each eye and the cortex. Thus the cortex contains a “map” or projection area, each point of which represents a point on the retina and therefore a point in visual space as seen by each eye. But the map is much too simple a model for cortical function. Vision tells much more than the location at which an object is seen. Visual tests show that other important features of an object such as its color, motion, orientation, and shape are simultaneously perceived. In monkey experiments, neurophysiologists have identified many types of cortical cells. each one responding selectively to these critical features. The two retinal maps are merged to form the cortical projection area. This merger allows the separate images from the two eyes to interact with each other in stereoscopic vision, binocular color mixture, and other phenomena. In addition to the projection areas on the right and left halves of the cortex, there are visual association areas and other brain regions that are involved in vision. Complex visual acts, such as form recognition, movement perception, and reading, are believed to depend on widespread cortical activity beyond that of the projection areas. *See also:* BRAIN.

Scotopic and photopic vision

Night animals, such as the cat or the owl, have eyes that are specialized for seeing with a minimum of light. This type of vision is called scotopic. Day animals such as the horned toad, ground squirrel, or pigeon have predominantly photopic vision. They require much more light for seeing, but their daytime vision is specialized for quick and accurate perception of fine details of color, form, and texture, and location of objects. Color vision, when it is present, is also a property of the photopic system. Human vision is duplex; humans are in the fortunate position of having both photopic and scotopic vision. Some of the chief characteristics of human scotopic and photopic vision are enumerated in the table.

Scotopic vision

This occurs when the rod receptors of the eye are stimulated by light. The outer limbs of the rods contain a photosensitive substance known as visual purple or rhodopsin. This substance is bleached away by the action of strong light so that the scotopic system is virtually blind in the daytime. Weak light causes little bleaching but generates neural inhibitory signals that lower the overall sensitivity of the eye. In darkness, however, the rhodopsin is regenerated by restorative reactions based on the transport of vitamin A to the retina by the blood. One experiences a temporary blindness upon walking indoors on a bright day, especially into a dark room or dimly lighted theater. As the eyes become accustomed to the dim light the scotopic system gradually begins to function. This process is known as dark adaptation. Complete dark adaptation is a slow process during which the rhodopsin is restored in the rod receptors of the retina. Faulty dark adaptation or night blindness is found in persons who lack rod receptors or have a dietary deficiency in vitamin A. These rare persons are unable to find their way about at night without the aid of strong artificial illumination. *See also:* VITAMIN A.

Dark adaptation is measured by an adaptometer, a device for presenting test flashes of light after various periods of time spent in the dark. The intensity of flash is varied to determine the momentary threshold for vision as dark adaptation proceeds. A 10,000-fold increase in sensitivity (that is, a reduction of 10,000 to 1 in the threshold intensity of flash) is often found to occur during a half-hour period of dark adaptation. By this time some of the rod receptors are so sensitive that only one elementary quantum (photon) of light is necessary to trigger each rod into action. A person can detect the presence of a flash of light that simultaneously affects only a few of the millions of rod receptors. Thus the scotopic sensitivity of the human eye approaches the ideal case of a receiver that is capable of responding to a single quantum of energy.

The variation of the scotopic threshold with wavelength of light is shown in the rod curve of **Fig. 2**. In spite of the variations in wavelength, the subject does not see any color when the intensity of the light is low enough to fall in the rod portion of the diagram. This scotopic vision is colorless or achromatic, in agreement with the saying that in the night all cats appear gray.

Normal photopic vision

Normal photopic vision has the characteristics enumerated in the table. Emphasis is placed on the fovea centralis, a small region at the very center of the retina of each eye.

Foveal vision. This is achieved by looking directly at objects in the daytime. In **Fig. 3**, the image of a small object at F falls within a region almost exclusively populated by cone receptors. These are so closely packed together in the central fovea that their density is about 130,000 per square millimeter. Furthermore, each of the cones in the fovea is provided with a series of specialized nerve cells that process the incoming pattern of stimulation and convey it to the cortical projection area. In this way the cortex is supplied with superbly detailed information about any pattern of light that falls within the fovea centralis.

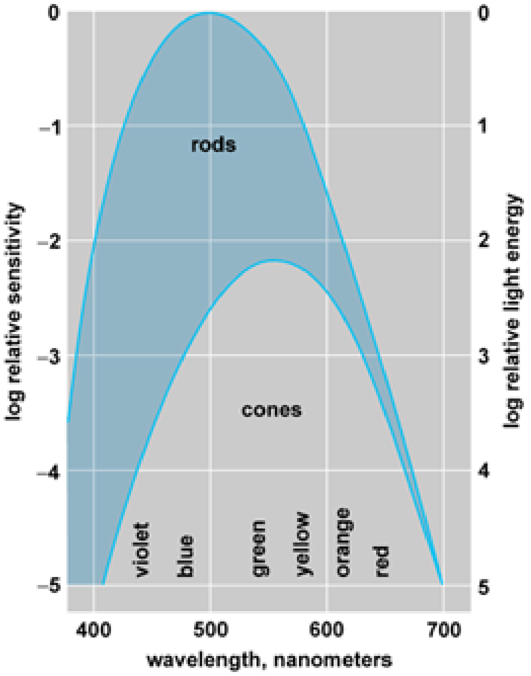

Fig. 2 Spectral sensitivity curves for human vision. The rod curve shows that scotopic vision, based on rhodopsin, is most sensitive to light of about 505 nm. The cone curve shows that photopic vision is generally less sensitive than scotopic vision, except for light at the red end of the spectrum.

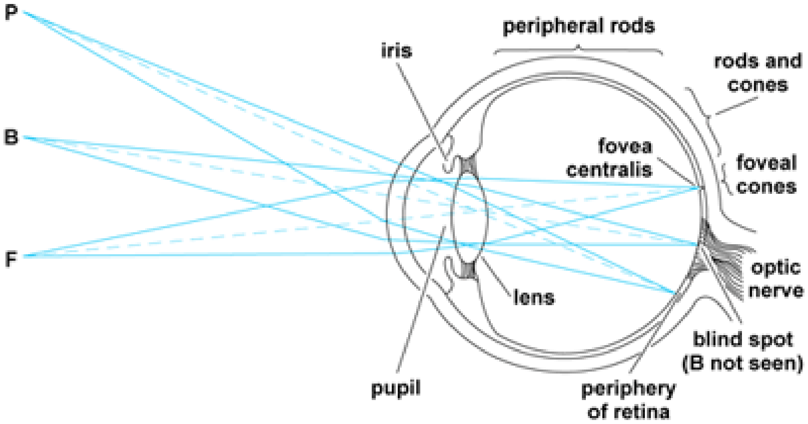

Fig. 3 Foveal and peripheral vision. Looking directly at F, the eye focuses the light from F on the central fovea, the region of clearest vision. P is seen poorly, and B not at all.

Peripheral vision. This is vision that takes place outside the fovea centralis (**Fig. 3**). As an example, look directly at a single letter at the center of a printed page. This letter, and a few letters immediately adjacent to it, appear clear and black because they are seen with foveal vision. The rest of the page is a blur in which the lines of print are seen as gray streaks. This is an example of peripheral vision. Vision actually extends out to more than 90° from center, so that one can detect moving objects approaching from either side. This extreme peripheral vision is comparable to night vision in that it is devoid of sharpness and color.

There is a simple anatomical explanation for the clarity of foveal vision as compared with peripheral vision. The cone receptors become less and less numerous in the retinal zones that are more and more remote from the fovea. In the extreme periphery there are scarcely any cones, and even the rod receptors are more sparsely distributed. Furthermore, the plentiful neural connections from the foveal cones are replaced in the periphery by network connections in which hundreds of receptors may activate a single optic nerve fiber. This mass action is favorable for the detection of large or dim stimuli in the periphery or at night, but it is unfavorable for visual acuity or color vision, both of which require the brain to differentiate between signals arriving from closely adjacent cone receptors.

Visual acuity. Visual acuity is defined as the ability to see fine details of an object. In **Fig. 1**, the small arrow at the back of each eye shows the image of the test object that is focused on the retina. Standard visual acuity is defined as the ability to see an object so small that the angle θ subtended at the eye is only 1 minute of arc, or 1/60 of a degree. At 20 ft (0.6 m) the size of such a test object is therefore only about 0.07 in., or 1.75 mm. The image of the object on the fovea (neglecting diffraction and optical aberrations that deteriorate the image) has a length of only 0.005 mm. Small as this is, it is twice the diameter of the smallest foveal cone receptor. One therefore comes to the conclusion that normal visual acuity approaches the limit imposed by diffraction and by the optical aberrations in the eye.

The specific forms of test object used for determining visual acuity yield different results. The angle θ in **Fig. 1** can be made so small that it represents the size of test object that can barely be seen by the normal eye. This angular size can be infinitely small in the case of a bright point seen against a dark background. The stars at night provide a good example of this, since they are so distant that their angular subtense at the eye is practically zero. A long dark line can be detected against a bright field (for example a flagpole seen against the sky) if it subtends 1 second of arc (1/60 of a minute) at the eye. On the other hand, letters of the alphabet, as used in optometric wall charts, need to be composed of black lines 1 minute thick in order to be recognizable to the normal eye. A similar value holds for the lines of a grating (with parallel black and white lines of equal width) when viewed under good illumination.

The apparent discrepancy between acuity for single points or lines on the one hand, and for more complex forms on the other hand, can be explained by the effects of optical diffraction. This is a phenomenon resulting from the wave nature of light. It means that no optical image can ever be completely sharp and clear. The retinal image of a star is not a point but a blurred circle of light. The diameter of this blurred image is never less than 1 minute of arc, no matter how small an angle the star itself may subtend. Thus the star is seen, provided that the blurred image is noticeably brighter than the surrounding field. In the case of a grating (black and white stripe pattern) the image of each line is blurred also. If the lines are too close (less than 1 minute) together, the blurred image of one overlaps the blurred image of the next and the separate lines cannot be resolved by the eye. One comes to

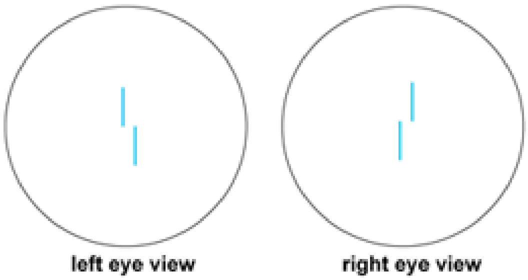

Fig. 4 **Vernier and stereoscopic discriminations of space.**

the conclusion, then, that the chief factors limiting the visual acuity of the fovea are (1) optical diffraction, (2) the ability to discriminate relative brightnesses within the images blurred by diffraction, and (3) the compactness of the pattern of cone receptors.

Space and time perception

Spatial and temporal effects are clearly apparent in the sense of sight. These two effects enable the individual to be oriented with regard to space and time in the surrounding world, especially in the perception of motion and distance. *See also:* PERCEPTION.

Space perception

Elementary forms of space perception are vernier and stereoscopic discrimination. Here, the eye is required to judge the relative position of one object in relation to another (**Fig. 4**). The left eye, for example, sees the lower line as displaced slightly to the right of the upper. This is known as vernier discrimination. The eye is able to distinguish fantastically small displacements of this kind, a few seconds of arc under favorable conditions. If the right eye is presented with similar lines that are oppositely displaced, then the images for the two eyes appear fused into one and the subject sees the lower line as nearer than the upper. This is the principle of the stereoscope. Again it is true that displacements of a few seconds of arc are clearly seen, this time as changes in distance. The distance judgment is made not at the level of the retina but at the cortex where the spatial patterns from the separate eyes are fused together. The fineness of vernier and stereoscopic discrimination transcends that of the retinal mosaic and suggests that some averaging mechanism must be operating in space or time or both. Furthermore, experiments with random dot stereograms demonstrate that the averaging mechanism can produce an impression of depth without visible contours in the retinal images of the two eyes.

The spatial aspects of the visual field are also of interest. As has been previously indicated, good acuity is restricted to a narrowly defined region populated by densely packed cones at the center of the visual field. A somewhat larger central region, in which the cones are somewhat more sparsely distributed, is capable of good color vision. Farther out, however, vision mainly is mediated by the rod receptors; color and form vision become

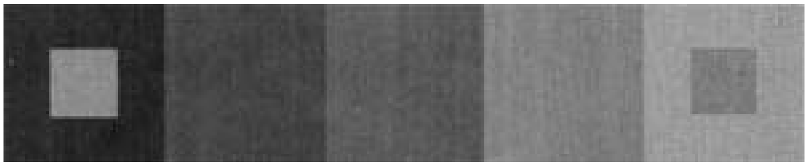

Fig. 5 **Simultaneous contrast. The two small squares are physically equal, and each of the five strips is uniform. Spatial inhibitory effects cause the right square to look darker than the left square and cause the apparent darkening of the portion of each strip that is adjacent to a lighter strip.**

extremely poor. In these peripheral regions area and intensity are reciprocally related for all small sizes of stimulus field. A stimulus patch of unit area, for example, looks the same as a patch of twice the same area and half the luminance. This high degree of areal summation is achieved by the convergence of hundreds of rod receptors upon each single optic nerve fiber. It is the basis for the ability of the dark-adapted eye to detect large objects even on a dark night.

In daytime vision, spatial inhibition, rather than summation, is most noticeable. The phenomenon of simultaneous contrast is present at a border between fields of different color or luminance. Thus a small square of gray paper appears darker on a light background than on a dark one; on a yellow background it appears bluish. The effect may originate in neural mechanisms of inhibition, such that stimulating a given region of a retina depresses the activity of regions immediately adjacent to it. This has the obvious effect of heightening contours and making forms more noticeable against their background (**Fig. 5**).

In photopic vision out of doors the eyes become light-adapted to an extent determined by such things as the time of day or the cloud cover. The luminance range of objects seen on a given day is typically no more than about 100 to 1 (two logarithmic units). Over this dynamic range the eyes appear to be capable of good spatial and temporal resolution, without the necessity for slowly adapting to the various levels of luminance.

Time perception

The temporal characteristics of vision are revealed by studying the responses of the eye to various temporal patterns of stimulation. When a light is first turned on, there is a vigorous burst of nerve impulses that travel from the eye to the brain. Continued illumination results in fewer and fewer impulses as the eye adapts itself to the given level of illumination. Turning the light off elicits another strong neural response. Afterimages are often seen at this time. A positive afterimage, resembling the original stimulus, is sometimes seen during the first fraction of a second after the light goes off. This is usually followed by a longer-lasting negative afterimage in which the color of the original object appears to be reversed. A clear afterimage may be produced by staring fixedly at the stimulus for at least a half minute, then turning away and “projecting” the afterimage against a white or gray screen. The retinal size of the afterimage remains constant, so that its size in inches on a screen is proportional to the distance of the screen from the observer (Emmert’s law). The afterimage is thought to arise chiefly from the fact that the affected region of the retina has been bleached, or otherwise changed photochemically, in such a way that its responses are different from those of the regions not stimulated. To some extent, however, visual aftereffects are due to central, rather than retinal, processes. *See also:* COLOR VISION.

The strength of a visual stimulus depends upon its duration as well as its intensity. Below a certain critical duration, the product of duration and intensity is found to be constant for threshold stimulation. A flash of light lasting only a few milliseconds may stimulate the eye quite strongly, providing its luminance is sufficiently high. A light of twice of the original duration will be as detectable as the first if it is given half the original luminance. However, even though two lights of the same energy may be equally detectable, a person may still be able to distinguish between them.

Voluntary eye movements enable the eyes to roam over the surface of an object of inspection. In reading, for example, the eyes typically make four to seven fixational pauses along each line of print, with short jerky motions between pauses. An individual's vision typically takes place during the pauses, so that one's awareness of the whole object is the result of integrating these separate impressions over time.

A flickering light is one that is going on and off (or undergoing lesser changes in intensity) as a function of time. At a sufficiently high flash rate (called the critical frequency of fusion, cff), the eye fails to detect the flicker, and the light pulses seem to fuse to form a steady light that cannot be distinguished from a continuous light that has the same total energy per unit of time. As the flash rate is reduced below the cff, flicker becomes noticeable, and at very low rates the light may appear more conspicuous than flashes occurring at higher frequency. The cff is often used clinically to indicate a person's visual function as influenced by drugs, fatigue, or disease. *See also:* PSYCHOLOGY.

Contrast sensitivity functions

Another approach to the study of vision is based on the concept of modulation, a term that has long been associated with periodic temporal changes in radio signals or in sound. But vision is particularly concerned, not with temporal variation, but with the spatial variations of light that characterize a pattern. The approach is to analyze pattern vision in terms of the contrast, or light modulation, that is measured within it. Furthermore, just as the methods of Fourier analysis have already yielded a good understanding of information transfer in radio transmission, the same methods are being applied with great success to pattern vision.

In Fourier terms, the simplest form of modulation is sinusoidal. Accordingly, an elementary form of visual pattern is the one in **Fig. 6**, where spatial frequency is 4 cycles per degree of visual angle (**Fig. 1**), average light intensity is I_{av}, and contrast (C) is $(I_{max} - I_{min})/(I_{max} + I_{min})$.

Sinusoidal gratings can conveniently be produced and controlled electronically on the face of a laboratory oscilloscope. To measure human contrast sensitivity, the contrast (C) of the grating is gradually reduced to

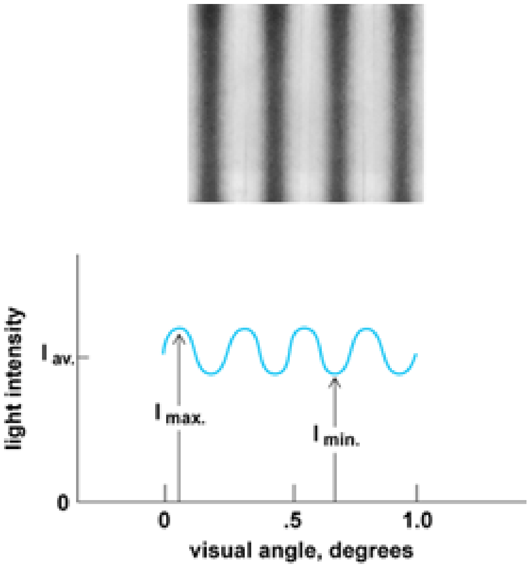

Fig. 6 Example of sinusoidal grating.

threshold (C_0), that is, to a point where the grating is barely distinguishable from a uniform field of the same average intensity. Contrast sensitivity is defined as the reciprocal of this threshold value of contrast.

Several important facts about vision emerge from the sinusoidal grating experiments. First, the entire range of spatial sensitivity can be explored in this way. A typical contrast sensitivity function for human vision (**Fig. 7**) peaks at about 3 to 4 cy/degree and becomes severely attenuated below 0.1 cy/deg and above 60 cy/deg. Second, prolonged viewing of a sinusoidal grating at high contrast causes a loss of contrast sensitivity for a grating of the same spatial frequency, but not for gratings of considerably higher or lower spatial frequency. This means that there are more or less separate “channels” in the visual system for responding to spatial frequency, just as there are separate channels for color, motion, and orientation. Third, neurophysiologists have already identified single cells in the visual systems of cats and monkeys that are tuned for spatial frequency. Relatively coarse tuning is found in the cat, particularly with cells at the level of the retina or the thalamus. But in the monkey, especially in the visual cortex, some cells are found that respond only within narrow limits to particular grating frequencies. Fourth, the Fourier analysis of visual function is highly practical and efficient. It yields a quantitative comparison between human and animal capabilities in pattern vision. Similarly, it can be used to describe the course and severity of visual defect in patients with eye disease. Optical and lighting engineers are now using it to evaluate the conditions most favorable for vision throughout the entire frequency domain. Finally, any given pattern or scene can now be described in terms of its Fourier spatial frequency components, just as music or speech has long been analyzed in terms of its component temporal frequencies.

Lorrin A. Riggs, Charles E. Sternheim

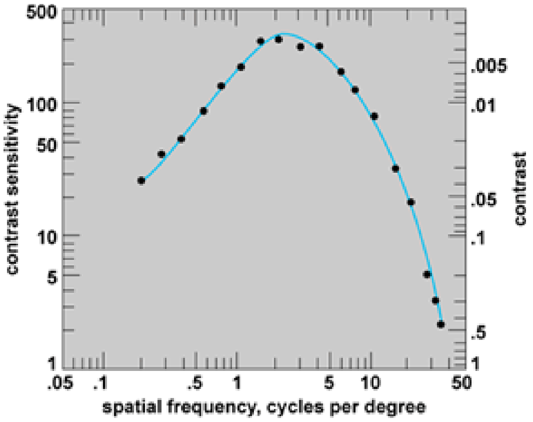

Fig. 7 **Contrast sensitivity curve for a human subject. (Credit: Based on data provided by F. W. Campbell and L. Maffei)**

Keywords

contrast; eye; fovea; foveal vision; peripheral vision; photopic vision; scotopic vision; sight; space perception; time perception; vision

Bibliography

H. Davson, *The Physiology of the Eye*, 4th ed., 1990

R. Held, H. W. Leibowitz, and H. L. Teuber (eds.), *Perception*, vol. 8 of *Handbook of Sensory Physiology*, 1978

D. H. Hubel, *Eye, Brain and Vision*, 1995

D. Jameson and L. M. Hurvich (eds.), *Visual Psychophysics*, pt. 4 of vol. 7, *Handbook of Sensory Physiology*, 1972

R. Jung (ed.), *Central Processing of Visual Information*, pt. 3 of vol. 7, *Handbook of Sensory Physiology*, 1973

R. Sekuler and R. Blake, *Perception*, McGraw-Hill, Boston, 2002

B. A. Wandell, *Foundations of Vision*, 1995

Additional Readings

G. Dagnelie (ed.), *Visual Prosthetics: Physiology, Bioengineering, and Rehabilitation*, Springer Science+Business Media, New York, 2011

T. Ledgeway, P. McGraw, and A. Simmers, What is the spatial integration area for global motion perception in human central vision?, *J. Vision*, 11(11):704–704, 2011 DOI: http://doi.org/10.1167/11.11.704

S. P. Liversedge, I. D. Gilchrist, and S. Everling (eds.), *The Oxford Handbook of Eye Movements*, Oxford University Press, New York, 2011

R. A. Pearson et al., Restoration of vision after transplantation of photoreceptors, *Nature*, 485(7396):99–103, 2012 DOI: http://doi.org/10.1038/nature10997

L. R. Squire et al., *Fundamental Neuroscience*, 4th ed., Academic Press, Waltham, MA, 2013

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