

Disciplines related to visual psychophysics and perception

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Visual psychophysics encompasses the beginning and the end of the visual processing chain. This is a great opportunity to learn more about the disciplines that deal with the intermediate stages. Let us start with the very beginning, dioptrics.

Optics of the eye

Here, you want to understand how an image forms on the retina by taking into account the refraction of the cornea and lens (the clear window panes of the eye through which the rays pass). An eye that is normally refracted is called emmetropic. When the ocular refraction is insufficient because the eye is either too long or too short, one speaks of shortsightedness (myopia) or farsightedness (hyperopia), respectively. To correct for these conditions, you need to wear glasses (concave -, convex +) to bring the focal point back onto the retina. Many Chinese and Japanese people are myopic possibly from reading at short distance and under poor lighting during childhood. Watch uncorrected people as they squint to improve their vision. This reduces the size of their pupil aperture, thereby affording greater depth of focus. The unit of refraction is diopter ($1/\text{focal length in meters}$). For example, when your near point is at 25 cm, your optician will prescribe a - 4 dptr lens (spherical correction). If the meridians in a star figure do not appear equally sharp, then you will require an additional correction for astigmatism (called a cylinder). You can find out whether or not you have it by rotating your glasses by 90 deg. Without these corrections, image quality will be suboptimal and the results of your experiment may be affected. Setting up a Maxwellian View System requires superb knowledge of physical and physiological optics. The classical work on the dioptrics of the human eye was done by Hermann von Helmholtz and Allvar Gullstrand (who received the Nobel Prize for it).

Luminance of the stimulus

To be able to specify the luminance, say, of a surface area, you need to measure it with a photometer. Chromatic stimuli require a spectral photometer whose sensitivity mimics the spectral sensitivity of the human eye in daylight (i.e., photopic). Such meters are expensive, but are mandatory for stimulus specification. A unit of measurement that is frequently used is candela per square meter (cd/m^2). There are many others that convert to each other. If you need to know the illumination on the retina, you must take the size of the pupil into consideration (i.e., troland). The contrast of a periodical grating pattern on the monitor can be calculated from the

maximum and minimum luminances according to the Michelson equation: $C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}}$; contrast sensitivity is the reciprocal of this term.

Signal transduction in the photoreceptors

Light entering the eye and hitting the photoreceptors starts a cascade of isomerization. This is the field of photochemistry, and it is a difficult one. Here it suffices to be able to calculate the fraction of bleached rhodopsin (rod pigment) for stimuli of different luminance and duration. William A. Rushton has provided easy formulas. A near 100 % bleach is seldom achieved and can take more than 1.5 hrs to recover until full sensitivity has been regained. Be careful not to damage the eye. People who lack vitamin A in their diet will gradually lose their ability to see at night. Make sure that your subjects eat enough fish and carrots. George Wald received the Nobel Prize for his discovery of the vitamin A cycle.

Histology of the retina:

The retina is comparable to light-sensitive wallpaper at the back of the eye, but it is more. It consists of a number of layers that process the stimulus before feeding it into the optic nerve. These layers are the horizontal cells, which integrate signals from many photoreceptors; bipolars, which interact with each other to set up lateral inhibition for image sharpening; amacrine cells, which disperse the information again; and, finally, retinal ganglion cells. Thus, there is no 1:1 telephone line from the receptor level to the ganglion cell level (and onward), except in the fovea centralis, where visual acuity is highest. Everywhere else, larger functional units are being formed with large numbers of receptors, funneling their output onto one ganglion cell (convergence); and many ganglion cells receiving their input from the same receptors (divergence). Ramon y Cajal was awarded the Nobel Prize for unraveling the circuitry of the retina.

The larger unit just mentioned is called the *receptive field* of a cell. It can be compared with the visual field (or acceptance cone) of that neuron. A retinal receptive field consists of a center and a concentric surround, which function antagonistically: light falling onto the center excites the neuron, whereas light falling onto the surround inhibits it (lateral inhibition). This type of cell is called an ON-center-neuron and mediates a percept of “brighter”. In the opposite arrangement of the receptive field, all signs are reversed: light inhibits the center, while it excites the surround (lateral activation). This type of neuron is called an OFF-center neuron and mediates a percept of “darker”. Typically, both kinds of neurons work at the same time, determining the brightness that you see. Keffer Hartline received the Nobel Prize for his discovery of the receptive field structure of optic nerve fibers.

Note that the receptive fields of the retina increase in size from central to peripheral vision. This explains the rapid decline of visual acuity as well as the increase of sensitivity for light and motion towards the mid- (and outer) periphery. Note that the density of cones is highest in the fovea, whereas the density of rods is highest between 10 and 20 degrees. Larger receptive fields make use of *spatial and temporal summation*, summing the excitation by all the quanta falling onto a given receptive field (5 arcmin² to 1 deg²) within a given duration of time (approx. 100 ms). In the compound eyes of insects, such as bees, receptive fields are invariant with eccentricity. So is (I believe) their visual resolution.

Ophthalmological function tests

Assume you can no longer see as well as you used to and therefore consult an eye doctor. He will first look at your fundus (retina) with a slit lamp and then check a number of functions, such as the following:

1. Foveal visual acuity

Resolution of central vision is measured using an acuity chart (Landolt C's, Snellen optotypes, sinusoidal gratings); a value of 20/20 is considered normal. A lesser value suggests short- or farsightedness or presbyopia. The latter typically begins at the age of 45 years and results from a loss of refraction due to a smaller range of accommodation of the lens (1 instead of 8 dptr). At a still higher age the lens may become cloudy (incipient cataract) impairing perceived contrast and color vision. In that case the eye doctor can no longer help by prescribing stronger glasses, but will eventually consider an artificial lens implant. There can be more serious reasons such as cell death due to a long-standing elevated pressure inside the eye (glaucoma) or loss of photoreceptors and nerve cells due to old age (macular degeneration, see below). Treatment of glaucoma should start as soon as possible and may require life-long therapy (drops, pills, surgery) and constant monitoring.

2. Color vision

The perception of color is typically ascertained by the use of the Ishihara pseudoisochromatic color plates. These are carefully produced plates with numerous dots of different color and size, which will reveal a number if read by a color-normal person. However, for someone suffering from color anomaly or color blindness, it will not be possible to see the (hidden) number, because all the dots have the same brightness and therefore will not stand out. There are other tests to check color vision, such as the Munsell D15 or D100 tests which require sorting color chips of equal

brightness and saturation according to their hue. Here, different color defects yield specific sorting patterns, which are used for diagnosis. A standard illumination is recommended for this task. The oldest and most accurate method involves mixing red and green in the Nagel anomaloscope to match unique yellow (575 nm). Color blindness can be a reason for withdrawal of your driver's license as you are liable to misread the color of the traffic light (red is always on top, green on the bottom, with yellow in the middle). It will also exclude you from several jobs where correct color perception is needed. Did you know that Viagra will slightly change your color vision towards blue?

3. Dark adaptation

In addition to the aforementioned procedures, your ophthalmologist may want to look at the kinetics of your eye to adapt to various light levels, including complete darkness. Imagine driving from the bright scene of a snowy day into the semi-darkness of a tunnel, you will not see much for some 20 seconds, before you feel comfortable. Lighting engineers attempt to compensate for this by a higher number of lamps at the mouth of the tunnel with a gradual decrease towards the middle and end. Conversely, when exiting from the tunnel it will take again a few seconds to overcome the glare. These percepts occur even if one considers the fast response of the pupil. When you track the progress of recovery by measuring the threshold as a function of time after a bleach, one typically obtains a bipartite curve. The instrument is called an adaptometer and the resulting curve is the dark adaptation curve. The upper branch refers to cone vision (photopic) and represents high visual acuity and color vision; it saturates at about 5 min and is followed by a lower branch referring to rod vision (scotopic) that represents high sensitivity, but absence of color vision. This latter branch reaches an asymptote as late as 45 min after the bleach. In a small range in between these two, both kinds of photoreceptors work simultaneously (mesopic vision). Light adaptation in the opposite direction proceeds much faster than dark adaptation. The total span of sensitivity change due to photochemical adaptation is as high as 7 log units (a factor of 10 million), enabling one to see the brightest as well as the dimmest light. However, cat eyes and the eyes of an owl provide an even higher sensitivity. These animals can see in the dark under condition, where you cannot.

In a small number of patients, the doctor may find an abnormal dark adaptation curve. A shorter and elevated upper branch suggests reduced day vision, while a shorter and elevated lower branch suggests reduced night vision. The first could be due to cone dysfunction, resulting in lower visual acuity and affected color vision (a relative central scotoma); the second might be due to rod dysfunction, causing a lower sensitivity in the dark and a smaller visual field (eventually approaching tunnel

vision). Both conditions are alarming when the doctor after more testing comes up with the diagnosis: age-related macular degeneration (AMD) or retinitis pigmentosa (RP). Very little can be done to stop these crippling diseases, although an early diagnosis may help. Repeated laser coagulations and injections into the eye ball are being used to prevent further loss of vision and ultimate blindness. There are heroic attempts under way to return vision to such patients by slipping a thin photosensitive foil underneath the retina to convert light into electric current and transmit the resulting signals to the optic nerve fibers and visual brain. But results so far have been controversial. There is a consolation: These two diseases, AMD and RP, afflict predominantly older people (who in former times may have died before the disease became manifest). The same holds for loss of eyesight from diabetes. Here the small ocular vessels break, bleed into the vitreous body and deprive the retina oxygen and nutrients. Fortunately, strict control of the amount of sugar in your blood can stave off blindness for many years. Retinal detachment is an added complication in advancing age, but may also occur in younger people. Flashes or dark spots are a telltale sign and prompt immediate treatment by an experienced eye doctor.

A complete lack of cones is quite rare and is due to a hereditary disorder. Such patients can read with high (12 x loupe) magnification, but have no color vision whatsoever, and exhibit pendular nystagmus due to the lack of a fovea. They are day-blind and avoid exposure to bright light by squinting and wearing dark glasses. On the other hand, their night vision is superb, sometimes even better than in normals. Read the chapter written by the best-researched rod monochromat Knut Nordby from Oslo on his childhood and youth, and the book by Oliver Sacks on the Island of the Color Blind. Fascinating!

4. Visual fields

A systematic check of the patient's visual fields belongs to the routines administered by an eye doctor. Different kinds of manual and automated perimeters are available, some requiring only a few min (central field), some much longer (central and peripheral field), for an examination. As a rule, a small moving light spot is introduced from the periphery of the visual field until the patient sees it. This is done from all different directions (meridians), using test spots of different size, to establish the boundaries of the visual field and Blind spot (kinetic perimetry). For a more detailed examination., light spots of varying intensity (and sometimes color) are briefly flashed in random locations of the visual field, and the absolute or differential threshold is measured to establish the sensitivity profile across a given meridian (static perimetry). Both procedures are invaluable functional tests to probe for ocular pathology, such as an enlarged Blind spot, an early sign of glaucoma. For reasons of

time, most practitioners rely on an abbreviated (inner) visual field plot, thereby possible missing pathology in the peripheral retina. Ask your friend to map your own visual fields and find out how much of it is binocular to provide depth perception.

5. Multifocal electroretinogram (ERG)

In addition to the psychophysical tests, your eye doctor may recommend recording the electrical currents generated by the retina in response to brief light flashes. This is an objective test that gives information on the functional status of small hexagonal sections of the retina when tested with light (no color, form, or motion involved). The tested sections increase in size towards the periphery roughly in accordance with receptive field size. Clinical diseases will show in a changed amplitude of the individual waves of the ERG-response.

Stereo-depth and contrast sensitivity in amblyopia

Until about 20 years ago, pediatric eye doctors used to see many children suffering from poor visual acuity and contrast sensitivity due to squint (cross-eyedness, strabismus). These children had inward or outward deviation of the optical axis of one eye, producing two rivaling images in the brain. If this condition is not treated well before entering school, by patching or surgery, amblyopia will result with a total and permanent loss of stereo acuity (suppression amblyopia). This is because the brain suppresses the weaker of the two images and as a consequence the binocular neurons in the visual cortex will atrophy or be rededicated to some other function. Often the contrast sensitivity of the amblyopic eye is affected together with stereo depth. Loss of visual function in one eye can also arise from astigmatism (meridional amblyopia) or unequal refraction of the two eyes (anisometropic amblyopia) in childhood. The worst visual damage will result from a milky cornea (leucoma) or lens (cataract) at birth as these conditions prevent clear image formation on the retina (deprivation amblyopia). Surgery soon after birth is indicated in many instances to avoid blindness. Such children will not be able to see when they are later operated upon, using a corneal or lens transplant. In the absence of stereovision, amblyopic patients – as one-eyed people - utilize secondary depth criteria such as apparent size, occlusion cues, motion parallax, and perspective for gauging distance.

Neurological complications

It is time now for you to change from your ophthalmologist to a cooperating neurologist, for example, if you are suffering from migraine. Migraines are difficult to treat and are sometimes attributed to a hysterical personality (which makes the

problem even greater). Migraine scotomata have been tracked as they traverse the visual field from the fovea to the periphery and have been interpreted in terms of a slow electrical wave moving across the receptive fields of the visual cortex. These zigzag or fortification phosphenes may reflect the activity of orientation-specific neurons and have been used to infer receptive field size as a function of retinal eccentricity. Other scotomata may be due to a tumor, gunshot wound, or hemorrhage (stroke) and can render an entire quadrant or half of the visual field blind in one or both eyes (hemianopia). From the presence of such deficits, the experienced physician can tell approximately where in the visual system (below or above the optic chiasm) the origin of the defect is located. Residual vision in and around scotomata from cerebral trauma has been reported to slightly improve under a strict regimen of rehabilitation. However, in Korean veterans who were followed up every 2 years over a long period of time the gain was negligible.

Multiple sclerosis (MS) caused by plaque formation and demyelination of the nerve fibers in the optic nerve is yet another neurological syndrome by which vision is affected. In MS-patients the conduction velocity of the two eyes may be differently affected, producing temporal delays and a percept of two flashes instead of only one. Such patients will see a pendulum that swings back and forth as rotating on an elliptical path in depth, because the brain interprets the time delay in terms of lateral disparity. This effect is known as the *Pulfrich phenomenon* and is used as a screening test in multiple sclerosis together with visually evoked cortical potentials (VECP).

Challenges and opportunities in neuropsychology

The field of neuropsychology has been boosted by the advent of functional neuroimaging (fMRI) and transcranial magnetic stimulation (TMS). Afflicted patients can now be studied noninvasively without opening the skull. (You still need a patient's consent, of course, in line with the Declaration of Helsinki.) Such patients may be seen as the result of an experiment by nature and offer unique insights into the visual system. For example, using these techniques the precise location of deficits in the living visual brain has become possible, such as cortical color blindness (cortical achromatopsia) in area V4, disturbed motion perception (akinetopsia) in area V5/MT, and face blindness (prosopagnosia) in the bilateral fusiform area. Disturbances of form vision have been located in the inferotemporal lobe, whereas impairment of spatial orientation has been attributed to the parietal lobe. These brain structures have therefore been called the “what” and the “where” systems.

Neo-Gestalt-neuroscience

The same techniques are being used to study brain architecture. Many of the visual

centers found by microelectrode studies in the cat and monkey are being confirmed and refined. The cortical magnification factor (overrepresentation of the fovea on the cerebral cortex) has been worked out in detailed studies, giving us a picture of a geometric stimulus as it is mapped on the surface of the brain. More is to come. Basic studies in conjunction with clinical studies help us to better understand vision and the visual brain. In this endeavor, psychologists are often on the forefront because they master more than one technique and also can put the individual findings from several disciplines better together. We are living in an exciting time, comparable to the beginning of single-cell neurophysiology in the early sixties that yielded an unprecedented neuronal inventory of visual feature detectors for brightness, color, orientation, motion, and depth (for which Hubel and Wiesel received the Nobel Prize). This, in a way, is comparable to the advent of Gestalt psychology at the beginning of the last century. It is to be expected that the laws of seeing, based on phenomenal observations, can soon be correlated with neuronal processes and mechanisms. Would you have imagined that advanced fMRI-analysis can reveal (an isomorphic replica) of the stimulus presented to the eye?