

## Pelvic Nerve

### Definition

The pelvic nerve connects the pelvic viscera (urinary bladder, urethra, distal bowel, vagina, uterine cervix) with the sacral S2-S4 (and in some species the lower lumbar) segments of the spinal cord. The nerve contains efferent autonomic neurons (mainly parasympathetic, but not entirely so), and also afferent nerves that convey sensory information to the central nervous system. It is responsible for the neural control of the hindgut, bladder and reproductive organs.

- ▶ Micturition
- ▶ Neurogenic Control
- ▶ Neurophysiology of Sexual Spinal Reflexes
- ▶ Visceral Afferents

## Pendular Nystagmus

### Definition

Nystagmus with a quasi-sinusoidal waveform (as opposed to “saw tooth” or “jerk” nystagmus in which there is alternation of slow and fast phases of nystagmus).

- ▶ Central Vestibular Disorders
- ▶ Nystagmus

## Penetrance in Inheritance

### Definition

In dominantly inherited disorders, penetrance refers to the proportion of persons with a mutation who show clinical symptoms. Complete penetrance refers to a situation where symptoms are present in everyone who has the mutation, and incomplete penetrance refers to a situation where symptoms are not always present in those with the mutation.

## Penumbra

### Definition

The marginally perfused area in the brain that surrounds the most deeply infarcted area during an ischemic stroke. This tissue is still viable if adequate perfusion can be maintained or restored.

- ▶ Ischemic Stroke
- ▶ Stroke

## PEPD

### Definition

- ▶ Paroxysmal Extreme Pain Disorder

## Percept

### Definition

The conscious experience of a sensory stimulus. The percept reflects stimulation of the sensory system (e.g. eye, ear, skin), but is also determined by higher-level cognitive processes (e.g. attention, memory).

- ▶ Perception

## Perception in Vision

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### Definition

Perception is the conscious experience of sensory stimulation. The perceptual process begins with the transformation of the external stimulus energy into the firing of neurons. The sensory signals originating in the sense organs are analyzed into different perceptual attributes such as pitch, color, form, or motion.

What is perceived depends not only on the raw sensory signal, but also on higher-level cognitive processes such as attention and memory. These processes are not always conscious, and they organize and interpret the information coming from the eyes (vision), ears (audition), nose (olfaction), tongue (taste), skin (tactile sense), and inner ears (vestibular senses). As a result, we perceive meaningful objects and events that are defined in both space and time. The perceptual process is very different from a mere image taken by a camera because objects and events are recognized and thereby linked to previously acquired knowledge stored in memory.

### Characteristics

Perception is our mind's window on the world. It enables us to create mental representations of objects (flowers, cars, etc.) or events (walks in a park, accidents, etc.), and enables us to interact with objects in the world. Vision is by far the most important sensory modality and this contribution is restricted to this modality. Nonetheless, most of the concepts presented here can be applied to other sensory modalities (audition, olfaction, taste, tactile and vestibular senses). The importance of vision is evident in the space allotted to it in the human neocortex: the primary visual cortex occupies about 15% of the neocortex, and more than 30 visual areas have been identified. Altogether, 60% of the human neocortex is involved in the processing of visual stimuli.

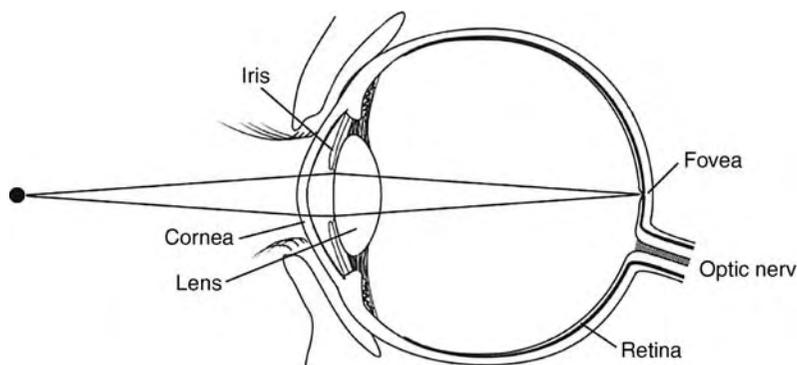
Intuitively, visual perception is a passive process; as soon as we open our eyes, we see the world around us. Another intuition about visual perception is that the basic units of visual perception are objects because we typically talk about objects (cars, flowers, etc.) when we report what we see. Both intuitions are wrong. Research in psychology and neurophysiology has shown that perception is a highly active process and that the attributes of an object such as its color or its movement are processed independently. The characteristic division of labor starts in the retina, and continues as visual

information is transmitted to the corpus geniculatum laterale (CGL) in the thalamus, and from there to the primary visual cortex. We will examine each of these stages in turn and show how complementary systems guarantee reliable perception under different conditions and for different purposes.

Light enters the eye through a small aperture, the pupil, and passes through the cornea and the lens before it reaches the retina (see Fig. 1).

Cornea and lens bring the image that is projected onto the retina into focus [1]. While the cornea has a larger focusing power (42 diopters), only the lens' focusing power (about 18 diopters) can be adjusted to bring objects into focus. To this end, the ciliary muscles contract and the curvature of the lens increases, a process that is called accommodation. A high curvature of the lens is associated with high focusing power that is necessary to project a clear image of nearby objects on the fovea. Across the lifetime, the lens loses elasticity and its maximal curvature decreases. As a consequence, a clear image would be projected on a plane behind the retina, but what is captured by the retina is blurred. This condition is known as presbyopia ("old eye"). Similar blurred retinal images result when the eye ball is too long or too short such that the focusing power of the lens is too weak or too strong, respectively. All these impairments may be corrected by glasses that either focus and thereby increase the focusing power of the optical system or disperse the light and thereby decrease its focusing power.

To be treated in the nervous system, the stimulus energy has to be transformed into electrical signals of neurons. In the visual modality, the process of transduction is achieved by two types of receptors: rods and cones. They are hidden behind a transparent layer containing amacrine, horizontal, bipolar and ganglion cells. The ganglion cells transmit the neuronal signals originating in the receptors to subcortical centers. Their axons leave the eye through an aperture in the retina



**Perception in Vision. Figure 1** A cross section of the human eye. The light passes through a small aperture (pupil) and is focused by the cornea and lens. The rays of light reach receptors in the retina that are hidden behind a translucent layer of cells (not shown).

devoid of receptors, the blind spot. Although no visual information is received in this region, we do not perceive a “hole” in our visual field when we close one eye. The visual system fills the void rather actively by extrapolating visual information from the neighboring retina.

Light entering the receptor engenders a biochemical cascade when hitting a photopigment contained in the receptor. The electrical potential of the receptor changes as a result of the cascade. This process is extremely sensitive: A single photon may change the potential of the receptor and light is perceived when only seven receptors are stimulated simultaneously. However, receptors respond only to electromagnetic energy at wavelengths between 400 and 700 nm. Small wavelengths evoke the color blue, medium wavelengths the colors green and yellow, and long wavelengths the color red. Wavelengths shorter (e.g. X-rays) than 400 or longer than 700 nm (e.g. radio waves) are not absorbed by the receptors.

The two receptor classes, rods and cones, have very different characteristics and involve different neural circuits. Rods are larger than cones and contain a photopigment that responds best to light at a wavelength of 500 nm. That is, light of this wavelength evokes a response more easily than light with higher or lower wavelengths. In contrast, cones may contain one of three different photopigments that differ in their preferred frequency: the short wave pigment (419 nm), the medium-wavelength pigment (531 nm) and the long wavelength pigment (558 nm). Taken together, the three cone types respond best to a wavelength of 560 nm. The difference in the preferred wavelength of rods and cones is evident in the Purkinje phenomenon: The colors in the lower part of the spectrum seem brighter (e.g. green objects appear more salient) when seen under conditions where rods are active compared to conditions where cones are active.

Rods enable us to see at low light intensities, but do not contribute to our visual experience in the daylight. The rod’s high sensibility is achieved by summing up signals across a large number of neighboring rods. While this strategy makes the system more sensitive, it produces a loss in spatial resolution. The activity of neighboring receptors cannot be discriminated and we only see blurred outlines in the dark. Also, the rod system cannot discriminate between different wavelengths and is therefore color-blind.

Cones are active during the daylight and do not contribute to nocturnal vision. They show far less summation across space than rods and thereby allow for the discrimination of spatial detail. Because the three types of cone receptors have different spectral sensitivities, they are differently activated by the incoming light. For instance, a monochrome yellow light of 575 nm will activate the long wavelength cone more than the medium and short-wavelength cones. The pattern of

activation of the three receptors is the basis for color vision and any physical stimulus that produces the same pattern of activity in the receptors will be perceived as equal (a so-called metamer color). For instance, a blend of medium and long wavelength is also perceived as yellow. If one of the cone types is missing due to a genetic deficiency, color vision is abnormal. Dichromats are predominantly male because the deficient gene is on the X-chromosome. They cannot discriminate between red and green and their color perception is limited to a continuum from blue to yellow or from blue to red, depending on the missing cone type.

The distribution of rods and cones across the retina is not uniform. While most of the retina contains both rods and cones, there is a small area located on the line of sight, referred to as fovea, which contains only cones. Few of the foveal cones (as few as one) converge on one ganglion cell and the density of cones and ganglion cells is higher than in the periphery. Therefore, the fovea is the retinal area with the highest spatial resolution (acuity). Most of what we consciously perceive is being projected on the fovea, in part because of the disproportionately large cortical representation of the fovea with respect to the rest of the retina. The cortical magnification of the fovea is due to the high density of ganglion cells in the fovea and to a larger cortical representation of ganglion cells projecting from the fovea.

The projections from the fovea to the cortex are highly ordered [2]. Adjacent locations on the retina will also be represented in adjacent locations in V1, a principle that is referred to as retinotopy. Cells in V1 combine the circular receptive fields of ganglion cells to form elongated receptive fields. The receptive field of a neuron refers to the area on the receptor surface from where the neuron receives information. While ganglion cells are maximally stimulated by small points of light, cells in V1 respond best to lines or bars. Cells in V1 have been classified according to their preferred stimulus. Simple cells in V1 respond best to bars of a certain orientation. Complex cells respond to oriented bars moving in a certain direction. End-stopped cells are selective to oriented bars of a certain length moving in a certain direction. Another characteristic of V1 is its organization into columns that share common processing characteristics. Location columns comprise neurons that respond to one particular location of the retina. Within such a location column, each eye is represented by two ocular dominance columns with neurons responding preferably to stimulation of the left or right eye. Finally, each ocular dominance column is composed of a complete set of orientation columns covering vertical to horizontal orientations. Neurons in an orientation column respond best to lines at a certain orientation.

While we do not directly perceive the representation of the stimulus in V1, V1 is necessary for conscious perception. Lesions of V1 lead to blindness in the

affected region. While this deficit, referred to as scotoma, eliminates conscious perception of stimuli presented in the respective visual area, it may not completely eliminate perceptual processing of those stimuli [3]. If patients who deny conscious perception of stimuli presented in the scotoma are forced to respond to these stimuli, their responses may show some residual sensitivity. For instance, they may be able to point to a stimulus presented in the scotoma with above chance (but far from perfect) performance. Even if cortical stimulus processing is precluded in this condition, retinal projections to a subcortical center in the midbrain are still intact. About 10% of the projections from the retina go to the superior colliculus, a structure that is also implied in the control of eye movements. Subcortical processing via this route may enable us to localize an object while circumventing consciousness.

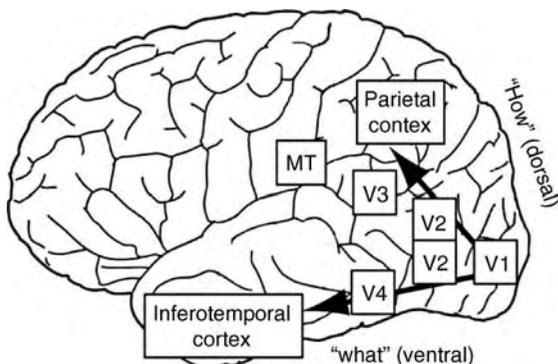
From V1, visual processing in the cortex continues along two major pathways: A ventral pathway from V1 to the inferotemporal cortex and a dorsal pathway from V1 to the posterior parietal cortex (see Fig. 2).

Even if there is considerable crosstalk between the two pathways, they show important functional specialization. The dorsal pathway is responsible for determining an object's location ("where" pathway), while the ventral pathway is responsible for determining an object's identity ("what" pathway). More recently, the dorsal pathway has been characterized as action pathway ("how" pathway) because it determines how a motor action is being carried out [4]. Obviously, information about where an object is located in space is crucial for successful motor interaction with it. A case study provided neuropsychological evidence for the distinction of "what" and "how." Patient DF suffered from damage to her ventral pathway after carbon monoxide poisoning. She was unable to identify simple geometrical forms or

to name objects, a condition known as visual form agnosia. For instance, she could not identify a screwdriver or describe the orientation of a slot. However, her actions toward these objects were unimpaired and she could place a card in the slot which cannot be done without information about its orientation. Presumably, information about the slot's orientation was available in the dorsal pathway that guided her actions, but not in the ventral pathway where conscious recognition of the object would usually take place. Conversely, patients with lesions in the posterior parietal area often show impairments in the visual guidance of actions, while object recognition is unimpaired.

The broad distinction between two visual pathways was further refined by the identification of cortical modules. Modules are cortical areas specialized in the processing of a particular perceptual dimension, such as form (see above), color, or motion in the visual modality. Damage to such a module results in an inability to perceive the respective dimension appropriately; a condition referred to as agnosia [5]. For instance, lesions of V4 make the perception of color difficult and patients perceive the world in shades of gray even if their cone system (see above) is intact. Lesions of V5 make the perception of motion impossible. In one such patient, moving objects appeared as static images in separate positions with no transitions between these positions. Thus, the patient was unable to pour a liquid into a glass because the liquid seemed to be frozen. Also, her interaction with other people was disturbed because she could not follow the movements of her interlocutor's mouth.

After demonstrating the modular, analytic processing of visual information, the intuitive unity of objects mentioned at the beginning requires further explanation. How can we perceive objects as basic units given that the brain analyzes objects into their component attributes? According to feature integration theory, the binding of attributes belonging to one and the same object requires attention [6]. That is, visual focal attention "glues" together the various properties of an object that are processed in a distributed manner in various modules. The role of attention has been studied using a paradigm referred to as visual search. In a typical trial, the observer is asked to look for a target, for instance a blue circle (features "blue" and "round"), and to indicate its absence or presence by a key press. The target is accompanied by a number of distractors. If the target can be discriminated from the distractors on the basis of a single attribute, the search is effortless and the target is readily detected even in a large set of distractors. For instance, the blue circle is easily seen among red circles. In this case, attention is not necessary to tie together the form and shape of the objects because the work of the color module is sufficient to signal the presence of the target. In this condition, the blue target is "salient" and will "pop out"



**Perception in Vision. Figure 2** Pathways from V1, in the occipital lobes, to the temporal and parietal cortices. The dorsal pathway from V1 to the posterior parietal cortex is important for object localization and action control. The ventral pathway from V1 to the inferotemporal cortex is important for object recognition.

from the red distractors. If, however, a conjunction of attributes has to be detected, the search is more effortful. For example, it is more difficult to detect a blue circle among blue squares and red circles. According to the feature integration theory, the observer has to scan one object after another and focus attention on each individual object to determine whether the required conjunction is present. The work of a single module is not sufficient (color and form is important), such that serial, attention-demanding integration of attributes is necessary. Consequently, reaction times in a conjunction search increase with the number of distractors.

There is general consensus that attention is necessary for conscious perception to occur. In a phenomenon called “inattention blindness,” observers fail to detect large changes in a picture if their attention is diverted by a secondary task [7]. For instance, observers may fail to notice a black gorilla walking through a scene if they are asked to count the passes of a team dressed in white playing against a team dressed in black. Even if the gorilla was clearly processed at the sensory level, it failed to be consciously perceived because the observer was focusing on white elements in the scene. Thus, both high-level cognitive and low-level sensory processes determine our visual world.

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## Perception, Philosophy

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### Definition

In current philosophical debates on perception the term “perception” refers almost exclusively to sense

perception, although it can be used (like the French “perception” or the German “Wahrnehmung” as well) for the acquisition of knowledge in general. Commonly there are taken to be five senses: sight, hearing, smell, touch and taste. Discussions concentrate for the most part on the sense of sight, however. Although it was at one time argued that perceptual verbs like “to see,” “to hear” etc. don’t refer to a kind of mental state, episode or event, because they qualify certain observations as successful in the same vein as “to win” does not describe an event or episode but reports an achievement, it is common now to acknowledge the existence of perceptual states and to take perceptual verbs as referring to those states.

### Description of the Theory

One may distinguish in the philosophy of perception basically two kinds of different issues: the first issue concerns the question of how perception as a particular mental phenomenon is to be construed. The second issue concerns epistemological questions, that is, questions dealing with the role of perception in the acquisition of factual knowledge. Making such a distinction is not to deny that both issues are connected in many ways. Indeed, it seems obvious that satisfying answers to the epistemological questions presuppose that at least some questions concerning the first issue have been settled. The main focus of this article will lie, however, on the first issue. The following questions are of particular importance: How is the representational content (henceforth simply: content) of perceptual states to be understood? Mental states in general represent the world to be a certain way; they tell us how the world is in certain respects. In this sense my perception of the tree outside the window represents the world to be a certain way. Correspondingly, there can arise two cases of misrepresentation here, illusion and hallucination. Illusions are cases where something in perception appears to be different from the way it actually is (e.g. a dummy of a tree appearing as a tree). In hallucinations objects appear to be there where no such object is present at all (e.g. the rats hallucinated by a delirious alcoholic). Accordingly, the philosophy of perception not only has to specify the nature of perceptual content (including the question as to whether or not it is similar to the content of other mental states like belief or thought) but has to give also an adequate account of illusion and hallucination. Mental states and their contents are related in various ways to one another and to our actions: we entertain beliefs with certain contents (e.g. that it will rain soon) because we have other contentful mental states (e.g. we perceive a sky full of grey and heavy clouds, we believe this to be a reliable sign of coming rain etc.) and we will therefore act in a certain way (we take our umbrella with us) and so on. This leads to the question of how perceptual content is related to other mental content and to the further question of what