NEUROPHYSIOLOGY

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Keywords: sensory receptors, sensory modalities, specific senses, motor control, associative and integrative functions, emotions

Contents

Summary

This article presents an overview of the functions of the nervous system. The topics dealt with include peripheral receptors, processing of sensory information in the central nervous system, the functions of specific senses, the central control of movement, brain associative and integrative functions, generation of emotions and theories about learning and memory.

1. Introduction and Overview of the Nervous System

The nervous system is a communication network that allows information transfer and processing in the organism. Neurophysiology is a discipline that deals with this aspect of animal and human physiology. The nervous system—a vast complex array of cellular networks—is connected to virtually all parts of the organism. It handles millions of bits of information in a time unit. The information reception from the environment and from the organism itself through different channels, and its primary processing in the central nervous system, is called sensory physiology. Based on this flow of information we can react in an appropriate manner to environmental and bodily events. Another important role of the nervous system is to control various bodily activities, such as motor functions and regulation of the secretion of endocrine and exocrine glands. Most of these activities are also initiated by stimuli emanating from sensory receptors. The integrative functions of the nervous system comprise complex processing of sensory information, association and interpretation of different types of signals, information selection and storage for future use, advance planning, and elicitation of behavioral responses. The nervous system, the brain in particular, is the most complex tissue in the organism. The understanding of the complexity of nervous system functions is therefore one of the greatest challenges for humanity.

The nervous system is divided into two major parts: the central and peripheral nervous systems. The central nervous system can be divided into seven major regions, which exhibit distinctly different functional propensities:

1. The spinal cord, the most caudal part, receives sensory information mediated by the peripheral nerves from various receptors, exteroceptors located in the skin, and from proprioceptors in the joints, muscles, and tendons. The spinal cord also mediates motor impulses from the higher regions to muscles and possesses motor functions of its own (i.e., reflexes).
2. The medulla oblongata directly above the spinal cord mediates both sensory and motor signals, but also includes centers responsible for the regulation of many vital autonomic functions, such as circulation, respiration, and digestion.
3. The pons in the metencephalon, above the medulla, conveys motor signals from the cerebrum to the cerebellum and possesses specific nuclei for the regulation of autonomic functions as well.
4. The cerebellum is a dorsal expansion of the metencephalon with a heavily gyrated surface. It is connected to the brain stem with three peduncles. It modulates motor functions, being mainly responsible for the learning of motor skills.
5. The mesencephalon, rostral to the pons, controls many sensory and motor functions and coordinates visual and auditory reflexes.
6. The diencephalon consists of two major parts: the thalamus and the hypothalamus. The former is an important link mediating information from the lower parts of the nervous system to the cerebral cortex and the latter an important center for the regulation of visceral and autonomic functions, and secretion of the endocrine glands.
7. The cerebrum is the most rostral part, consisting of a pair of cerebral hemispheres. The relatively great mass of the cerebral hemispheres in comparison to other brain parts and, in particular, the expanded surface of the cerebral cortex, are characteristics of the human brain. The surface of the cerebrum—the cerebral cortex—is heavily gyrated in man, greatly expanding its surface area. The cerebral cortex is the major region for sensory coding, association, and interpretation, and is responsible for the performance of motor and integrative functions, and cognition. The basal ganglia, which participate in the regulation of motor functions, the hippocampus, obviously important for information storage and memory, and the amygdaloid nuclei, which underlie

the generation of different emotional states, are located in the interior of the cerebral hemispheres.

All nerve cell processes outside the central nervous system, with their associated cellular elements, are included in the peripheral nervous system. Their main role is to connect the central nervous system to the peripheral organs from which information is received and/or the functions of which are regulated by the central nervous system. The autonomic nervous system is a part of the nervous system designed to control visceral functions of the body. It consists of elements from both the central and peripheral nervous system. The centers located in the spinal cord, brain stem, and hypothalamus activate the autonomic nervous system. However, the activation of the above centers is partly under the control of the limbic cerebral cortex. Peripheral ganglia are also essential parts of the autonomic nervous system. The autonomic nervous system comprises two major subdivisions: the sympathetic and parasympathetic parts. Their functions are, in most cases, the opposite of each other (see *Autonomous Neural Regulation*). (For the main cell types of the nervous system, neurons, and glial cells, see *Structural Neurobiology*. For the functions of neurons responsible for impulse generation, propagation, and transmission, see *Neurons, Action Potentials, and Synapses*. Impulse transmission from neuron to neuron is mediated electrically in the minority of synaptic junctions, while the majority are chemical in nature, employing specific substances as mediators—neurotransmitters—see *Neurotransmitters and Modulators*.)

2. Sensory Functions

2.1. Peripheral Receptors

A variety of sensory receptors mediate information from the environment and from the interior of the body to the central nervous system (see Table 1). Different forms of energy first evoke analogical changes in their membrane potentials (receptor potentials). These are then converted into digital signals—action potentials—which are propagated along the neuronal plasma membranes over long distances to reach their destination in the central nervous system. The sensory receptors are adapted to respond to one particular type of energy and therefore exhibit a whole spectrum of structural and functional characteristics. The particular form of energy to which a receptor is most sensitive is known as its adequate stimulus. For instance, the adequate stimulus for a touch receptor is mechanical force and for a photoreceptor is electromagnetic radiation—light. A receptor responds to its adequate stimulus at a much lower threshold than to other types of stimuli, but responses to unspecific stimuli commonly occur at high stimulus intensities. The stimulus-evoked excitation of receptors most often opens ion channels in their plasma membranes, resulting in depolarization (see *Ionic Channels of the Excitable Membrane*), but light impinging on photoreceptors closes ion channels and causes hyper polarization.

Receptor type	**Sensory modality**	**Location**
Photoreceptors	Vision	Eye, retina, rods and cones
Hair cells	Hearing	Ear, organ of Corti

Hair cells	Linear acceleration	Ear, utriculus and sacculus
Hair cells	Angular acceleration	Ear, semicircular canals
Taste receptors	Taste	Oral cavity, taste buds
Olfactory receptors	Smell	Nasal olfactory areas
Naked nerve endings	Pain	Skin and other tissues
Nerve endings	Cold	Skin
Nerve endings	Warmth	Skin
Specialized neurones	Temperature	Hypothalamus
Nerve endings	Touch and pressure	Skin
Nerve endings	Position and movement	Joints
Nerve endings	Fiber length	Muscle spindles
Nerve endings	Tension	Golgi tendon organs
Glucoreceptors	Blood glucose level	Hypothalamus
Osmoreceptors	Osmotic pressure	Hypothalamus
Glomus cells	Oxygen partial pressure	Carotic and aortic bodies
Stretch receptors	Fiber length	Heart atria
Stretch receptors	Venous blood pressure	Large veins
Nerve endings	Lung inflation	Lung tissue
Nerve endings	Arterial blood pressure	Carotic and aortic sinuses
Specialized receptors	Hydrogen ion concentration	Medulla oblongata

The nerve endings in the skin form histologically recognizable Pacini's corpuscles, Merkel's disks, Ruffini's endings, Krause's end-bulbs and Meissner's corpuscles. These structures seem to function as mechanoreceptors responding to tactile stimuli. As an example, the structure of a Pacinian corpuscle is shown in Figure1.

Table 1. Sensory receptors, their modalities and locations

Notes: The nerve endings in the skin form histologically recognizable Pacini’s corpuscles, Merkel’s disks, Ruffini’s endings, Krause’s end-bulbs, and Meissner’s corpuscles. These structures seem to function as mechanoreceptors responding to tactile stimuli. As an example, the structure of a Pacinian corpuscle is shown in Figure1.

The receptors can be classified in different ways. One traditional classification divides them into teleceptors, which receive information from a distance, exteroceptors, which respond to stimuli near the body, and proprioceptors, which respond to stimuli from the interior of the body. Some receptors are located in specific sensory organs ("specific senses"), whereas others are more widely distributed in the organism. A number of receptors responsible for different sensory modalities are compiled in Table 1 with their adequate stimuli and locations in the body. Within certain limits the sensory sensation is approximately related to the logarithm of the magnitude of stimulus (the classic Feber-Wechner's law). More accurately the intensity of sensation (R) is described by the equation $R = KS^A$, in which S is the magnitude of stimulus and K and A constants. The frequency of action potentials generated approximately obeys a similar equation.

Adaptation is a characteristic propensity of many receptors. In rapidly adapting receptors, a stimulus produces only a short-lived response that rapidly fades out during continuous stimulation. In slowly adapting receptors, the response is a repetitive discharge on prolonged stimulation. The first type of receptor is adapted to detect fast changes and the latter type is best suited for the maintenance of constant responses to internal or environmental effects. The receptive field of a receptor defines the region in which stimulation elicits its activation. The receptive fields of adjacent receptors frequently partly overlap. In the sensory (and also motor) pathways, divergence at various second- or third-order levels provides a means to generate receptive fields at the upper levels of the central nervous system that are larger than those of the first-order afferent neurons. At the same time, convergence of other neurons yields a certain degree of overlap (see Figure 1). Inhibitory mechanisms are also very important for the accurate localization and discrimination of different stimuli. Recurrent axon branches from adjacent neurons in a pathway can inhibit each other, providing a phenomenon known as lateral inhibition. With the aid of lateral inhibition, the targets of motor pathways can be similarly focused.

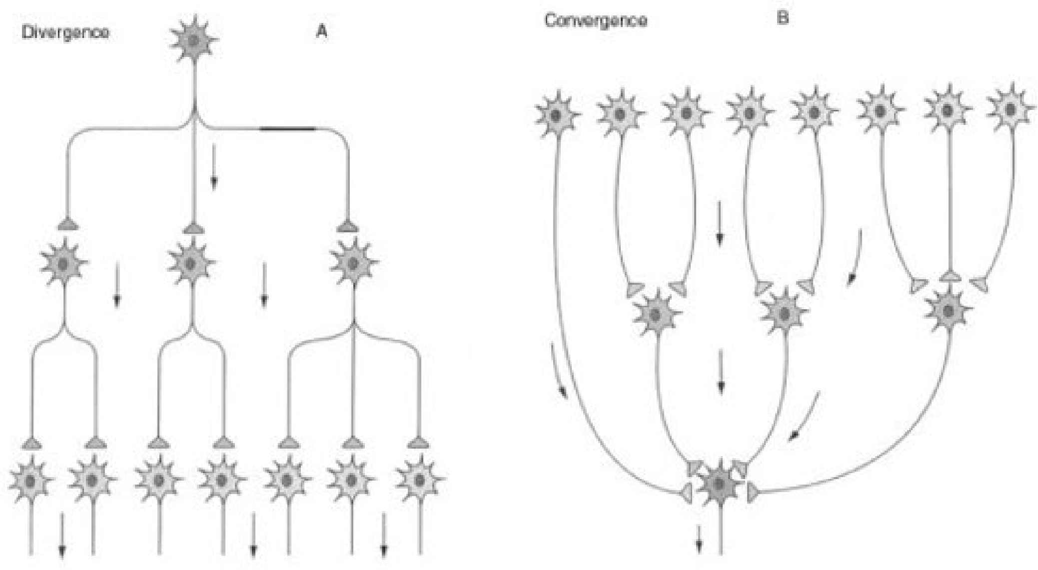

Figure 1. Diverging (A) and converging (B) neural networks
Notes: One primary afferent neuron is able to activate by means of divergence several second-order neurons, which then each in turn activate several third-order neurons. On the other hand, in the case of convergence, several first-order neurons target on one third-order neuron.

The best-characterized receptors are located in the skin where a variety of receptors have been described by histological methods. The specificity of these receptors to different types of stimuli is not yet fully established. Figure 2 shows the structure of a typical skin receptor: the Pacinian corpuscle. In the skin, the receptor density is generally directly related to the ability to locate stimuli accurately and to discriminate between two stimuli that are close to each other. The number of second-order and third-order neurons is correspondingly in proportion to the density of first-order afferent neurons. At the most central level in the cerebral cortex, the size of the areas representing the different parts of the body is proportional to the density of the first-order sensory neurons. A sensory homunculus drawn over the sensory cerebral cortex, therefore, does not reflect the relative sizes of various body parts, but the number of sensory receptors in them.

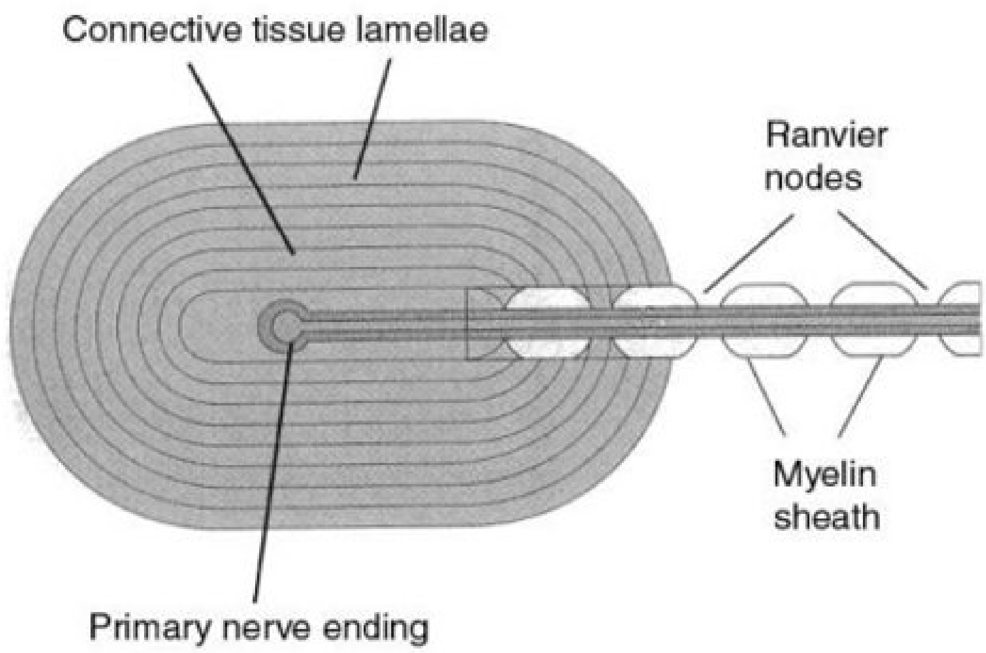

Figure 2. Structure of a Pacinian corpuscle

Notes: The primary nerve ending is encapsulated with concentric onion-like lamellae of connective tissue, which function as amplifiers of the mechanical pressure applied to the receptor. The pressure dislodges the layers and that generates alterations in the nerve membrane potential (generator potentials), which then evoke a burst of digital action potentials in the first node of Ranvier inside the corpuscle.

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Bibliography

Davies A., Blakeley A.G.H., and Kidd C. (2001). Chapter 3: Neurological communication; Chapter 4: Special senses and higher functions. *Human Physiology*, pp. 137–369. Edinburgh, UK: Churchill Livingstone (Harcourt Publishers). [An easy basic textbook with chapter summaries and clinical examples.]

Ganong, W.F. (2001). Section III, Chapters 6–16: Functions of the nervous system. *Review of Medical Physiology, 20th Edition*, pp. 123–269. New York: McGraw-Hill. [A detailed textbook of human physiology.]

German W.J. and Stanfield C.L. (2001). Chapter 8: The nervous system: central nervous system; Chapter 9: The nervous system: sensory systems; Chapter 10: The nervous system: autonomic and motor systems. *Principles of Human Physiology*, pp. 224–332. San Francisco: Benjamin Cummings. [A textbook of basic human physiology, easy to read, with questions and CD software for self-study.]

Guyton A.C. and Hall J.E. (2000). The nervous system. Unit IX: general principles and sensory physiology. Chapter 45: Organization of the nervous system: basic functions of synapses and transmitter substances; Chapter 46: Sensory receptors: neuronal circuits for processing information; Chapter 47: Somatic sensations I—general organization: the tactile and position senses; Chapter 48: Somatic sensations II—pain, headache, and thermal sensations. Unit X: The special senses. Chapter 49: The eye I—optics of vision; Chapter 50: The eye II—receptor and neural function of the retina; Chapter 51: The eye III—central neurophysiology of vision; Chapter 52: The sense of hearing; Chapter 53: The chemical senses—taste and smell. Unit XI: Motor and integrative neurophysiology. Chapter 54: Motor functions of the spinal cord—the cord reflexes; Chapter 55: Cortical and brain stem control of motor function; Chapter 56: The cerebellum, the basal ganglia, and overall motor control; Chapter 57: The cerebral cortex—intellectual functions of the brain, and learning and memory; Chapter 58: Behavioral and motivational mechanisms of the brain—the limbic system and the hypothalamus; Chapter 59: States of brain activity—sleep, brain waves, epilepsy, psychoses; Chapter 60: The autonomic nervous system, and the adrenal medulla; Chapter 61: Cerebral blood flow, the cerebrospinal fluid, and brain metabolism. *Textbook of Medical Physiology, Tenth Edition*, pp. 512–715. Philadelphia: Saunders. [A classical textbook of human physiology, relatively easy to read.]

Haines D.E. (ed.) (1997). *Fundamental Neuroscience*. New York: Churchill Livingstone. [A thorough presentation of neuroscience with somewhat complicated illustrations.]

Kandel E.R. Schwartz J.H., and Jessell T.M. (ed.) (2000). *Principles of Neural Science, Fourth Edition*, New York: McGraw-Hill. [A comprehensive textbook of all aspects of neural science.]

Moffett D., Moffett S., and Schauf C. (1993). Section II: Nerve and muscle. *Human Physiology, Second Edition*, pp. 159–353. St Louis: Mosby. [A typical textbook of physiology with self-study questions.]

Purves D., Augustine G.J., Fitzpatrick D., Katz L.C., LaMantia A.-S., and McNamara J.O. (ed.) (2000). *Neuroscience, Second Edition*, 681 pp. Sunderland, MA: Sinauer Associates. [A systematic textbook of neuroscience.]

Rhoades B.A. and Tanner G.A. (1995). Part 2: Neurophysiology. *Medical Physiology*, pp. 59–146. Boston: Little, Brown. [A simple text of basic human physiology, including review exercises with answers for self-study.]

Silverthorn D.U. (1998). Chapter 8: The nervous system; Chapter 9: The central nervous system; Chapter 10: Sensory physiology; Chapter 11: Efferent peripheral nervous system: the autonomic and somatic motor divisions; Chapter 11: Muscles; Chapter 13: Integrative physiology of body movement, *Human Physiology: An Integrated Approach*, pp. 202–382. Upper Saddle River, NJ: Prentice-Hall. [A relatively simple textbook with good illustrations.]

Willis W.D. Jr. (1993). Section II: The nervous system. *Physiology, Third Edition* (ed. R.M. Berne and M.M. Levy), pp. 91–278. St Louis: Mosby. [A basic text of human physiology with chapter summaries.]

Biographical Sketches

Simo S. Oja is Professor in Biomedical Sciences (physiology), University of Tampere, Director of the Tampere Brain Research Center, and Docent in Biochemistry, University of Oulu, Finland. He was born in 1939 in Kärkölä, Finland. He obtained his Master of Science (M.Sc.) in 1962; Medical Doctor (M.D.) in 1964; Licentiate in Philosophy (Ph.L.) in 1965; Doctor of Philosophy (Ph.D.) in 1966; Doctor of Medical Sciences (M.Sc.D.) in 1967 (all at the University of Helsinki); and Master of Civil and Criminal Law (M.L.) in 1988 (University of Turku).

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He has been Vice President of Finnish Physiologists' Association since 1996. He was a Member of the Executive Committee of the Finnish Brain Research Society from 1984 to 1992, and again from 1998 to the present. Found qualified and competent for many professorial posts in Physiology, Pharmacology, Biochemistry, and Medical Chemistry in several Finnish universities. Editor *Neurochemical Research*, 1999–present. Has participated in more than 100 international meetings, congresses, and symposia in physiology, pharmacology, biochemistry, and neurosciences since 1974. Has produced about 250 original scientific publications on chemistry, physiology, and pharmacology of brain neurotransmitters.