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Introductory Chapter: Organization and Function of Sensory Nervous Systems

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1. Introduction

Thomas Heinbockel

This chapter introduces the concept of the sensory nervous system and briefly discusses the value of model organisms in enhancing our understanding of the evolution of sensory systems. The world around us continuously stimulates our senses. These stimuli come in different varieties (modalities) such as light, sounds, smells, tastants, and somatic sensation (touch, pain, pressure, vibration, heat, cold). Our corresponding senses communicate the outside world to the inside of our body with the help of specific receptors. These are part of the nervous system and connect the periphery with the brain. The nervous system, in turn, can respond to incoming information by generating adaptive signals and behaviors. It is essential for all organisms to be able to perceive stimuli from the environment and to subsequently process and integrate these stimuli with the help of our sensory systems. Animals including humans have a need for information about the processes that go on inside of our body as well as on the outside to maintain homeostasis and to properly respond to the organism's bodily functions and surrounding environment [1].

All of us are familiar with the well-known senses such as seeing, smelling, tasting, and hearing. In addition, animal species have taken advantage of other environmental stimuli for orientation and survival and, thus, provide us with less-known examples of sensory systems, for example, echolocation in bats, heat sensation in snakes, magnetic compass orientation in migratory birds, or polarized light perception in insects. Consequently, the sensory nervous system can show exquisite differences between the many existing animal species. Nevertheless, researchers have found astounding similarities in sensory processing even among members of distant animal taxa with respect to the structure and function of the sensory pathways.

Several fundamental rules govern how the sensory nervous system processes stimuli in different modalities [2]. In each case, specialized receptor cells transduce the environmental signal into an electrical or a neural signal that is sent to the brain by afferent nerve fibers. Both the



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receptor cells themselves as well as the synaptic targets of the receptor cells, neurons in the brain, are capable of encoding specific attributes of the stimulus such as its quality and quantity. In some cases, receptor cells and central neurons can transmit information about the temporal dynamics of the stimulus (intermittency) and its location in space. As far as the transmission of sensory information from one relay station in a sensory pathway to the next is concerned, neighboring groups of neurons in a given relay station maintain the spatial relationship of receptor cells in the peripheral sense organs. This has been demonstrated in our spatial senses such as vision and touch. This topological organization helps the organism to convey spatial information about sensory stimuli [3]. Nevertheless, it would be a falsehood to assume that sensory systems convey a perfect and complete picture of the world around us [4]. Even though receptor cells at first glance appear to function as physical devices, they are meant simply to help us make inferences about the world rather than provide us with correct measurements. Neurons along a sensory pathway encode stimulus information and transform this information based on computational rules inherent in the neurons and their synaptic connectivity [4]. Therefore, the information that reaches the brain is not simply a mirror reflection of the environment; rather, the information is exposed to multiple levels of processing.

2. Divisions of the nervous system

How does the sensory nervous system fit into our understanding of the nervous system? A standard way to distinguish different parts of the nervous system is to refer to the central versus peripheral nervous system [5, 6]. The central nervous system includes the brain and spinal cord with about 86 billion neurons and trillions of glial cells in the brain. The peripheral nervous system consists of the nerves and ganglia outside of the brain and spinal cord, and it can be divided into the somatic and the autonomic nervous system. The somatic nervous system comprises peripheral nerve fibers, namely sensory nerve fibers (afferent fibers) that send sensory information to the central nervous system as well as motor nerve fibers (efferent fibers) that project to skeletal muscles. The somatic nervous system affords us voluntary control over our skeletal muscles [2, 6]. In contrast, the autonomic nervous system controls smooth muscles of the viscera (internal organs) and the digestive tract as well as sweat glands, salivary glands, kidney, bladder, pupil, and heart muscle. As the name implies, it works automatically (autonomously), without a person's conscious effort, that is, we do not have a voluntary control over the autonomic nervous system. Accordingly, it is also called the involuntary or the vegetative nervous system. The autonomic nervous system comes in two opposing parts, sympathetic and parasympathetic. The sympathetic division stimulates bodily processes in response to information about the body and the external environment received by the autonomic nervous system, whereas the parasympathetic division has an antagonistic effect by inhibiting bodily functions.

Principally, the sensory nervous system with its different sensory systems is part of the peripheral nervous system or, better, it starts in the periphery and ends in the central nervous system. As a whole, the sensory nervous system detects and encodes stimuli and then sends signals from receptors, that is, sense organs or simple sensory nerve endings, to the central

nervous system, that is, it transduces environmental signals into electrical signals that are propagated along nerve fibers. In contrast, the motor systems respond to information provided by the sensory systems to generate movements and other forms of behavior. The main function of the sensory nervous system is to inform the central nervous system about stimuli impinging on us from the outside or within us. By doing so, it informs us about any changes in the internal and external environment. The central nervous system integrates the sensory information and communicates the information to target organs in our body. Therefore, a given sensory system comprises receptor cells in sense organs, neurons that project from sense organs to the brain, and specific brain areas that process the afferent information coming from the periphery. For each of the five classic senses (vision, touch, hearing, smell, and taste), a corresponding cortical area exists in the brain [5] referred to as sensory cortex, namely visual cortex, somatosensory cortex, auditory cortex, olfactory cortex, and gustatory cortex. Our brain also houses a vestibular cortex to process information from the vestibular organs, the utricle and saccule with the maculae, and the semicircular ducts with the crista ampullaris.

In addition to the sensory cortices, the brain or, more specifically, the cerebral cortex is involved in the control of voluntary movement, for example, in the frontal lobe [6]. Parts of the brain are responsible for encoding sensory information and controlling motor behavior. These are the primary sensory and motor cortices, and they constitute only about one-fifth of the cerebral cortex [2]. Not all brain areas can be assigned easily to either sensory or motor functions. These areas are involved in processing complex stimuli, forming relations between objects and planning adaptive responses including memory formation. The functions are referred to as cognition and are carried out in the association cortices in the parietal, temporal, and frontal lobes such as the prefrontal cortex, posterior parietal cortex, and inferotemporal cortex [2].

3. Relevance of the sensory nervous system

As pointed out so poignantly by Barth et al. [7], "there is no life without sensors and sensing." The authors emphasize that even in bacteria without a nervous system, sensory performance is in place. Sensing and sensory systems are a characteristic property of living animals and have evolved over millions of years by selective pressures to develop many sense organs for specific tasks with magnificent precision [1]. As a result, animals use a stunning diversity of sensory systems to extract information from their environment [8] and have many sensory abilities not know to humans such as ultraviolet, infrared, ultrasound, electromagnetic reception, and skeletal strain detection [7]. On the one hand, the differences between the sensory systems in terms of complexity are obvious. On the other hand, despite all the differences, there are commonalities that have been discovered in sensory systems and the brains [1]. As indicated by these authors, while some animals such as insects and mollusks may vastly differ from humans, they share a surprising number of basic properties of living organisms. The similarities extend to brain functions such as learning and memory and advanced cognitive abilities which traditionally have been associated with primates rather than snails, bees, or birds.

4. The olfactory system

A prominent example of the commonalities of sensory systems is provided by the olfactory system that has been studied in vertebrates and invertebrates for several decades [9–18]. The similarities start in the periphery with olfactory receptor cells located in the olfactory epithelium in the nose of vertebrates or in the paired antennae of insects. The receptor cells are adapted to detect a vast array of odorants by means of receptor proteins that are positioned in the membranes of the receptor cells. The olfactory receptor cells are associated with various types of sensilla in invertebrates (e.g., insects) [19] or the olfactory epithelium lining a portion of the nasal cavity of vertebrates (e.g., mammals) [20]. Individual receptor cells are specialized to respond to one or a few different odorants by expressing one member of a large gene family of olfactory receptor proteins as shown for rodents [20]. Likewise, Clyne et al. [21] and Vosshall et al. [22] identified a novel family of seven transmembrane-domain proteins, which are encoded by 100-200 genes and are likely to function as Drosophila melanogaster olfactory receptors. An individual olfactory receptor cell in the antenna of D. melanogaster is thought to express one or a few of the candidate olfactory receptor genes, and, therefore, each olfactory receptor cell is functionally distinct [23]. In insects, an antennal receptor cell in male moths might respond to only one component of several chemicals that make up the sex pheromone released by the conspecific females [24–26]. The olfactory receptor cells send their axon to the first central relay station for olfactory information processing in the brain and form synaptic contacts with central neurons. In vertebrates, this takes place in the olfactory bulb; in insects, it occurs in the antennal lobes of the deutocerebrum [27]. In both, the olfactory bulb and the antennal lobes, olfactory information is processed in brain modules, the olfactory glomeruli. Each glomerulus is a discrete anatomical and functional unit and serves as an anatomical address dedicated to collecting and processing specific molecular features about the olfactory environment, conveyed to it by olfactory receptor cell axons expressing specific olfactory receptor proteins [11, 12, 28-30]. Thus, the glomeruli in the antennal lobes of insects and the olfactory bulbs of vertebrates are organized chemotopically [30-35], analogous to visuotopy, in visual systems, and tonotopy, of auditory systems. In both vertebrates and insects, olfactory information is extensively processed at the level of the glomeruli through feedforward and feedback inhibition and modulation provided by centrifugal neurons. Information is subsequently conveyed to a higher-order olfactory center such as the olfactory cortex in vertebrates or the mushroom bodies and lateral horn in insects [36, 37]. These circuit similarities among distant taxa demonstrate the convergence of basic brain mechanisms in sensory systems.

5. Animal model systems

Which animal models are used to study sensory nervous systems? The question relates to finding the best animal model to study a particular sensory system. Most biological and biomedical research focuses on a small number of animal models, the Core Four, mice, zebrafish, fly (*Drosophila*), and worm (*Caenorhabditis*) because of their genetic tractability

[38]. Many other animal species are being used to determine the structure and function of a specific sensory system. This is in part mandated by the fact that not all animal species are equipped with the same senses. And even if they possess a specific sensory system, it might be rudimentary in its anatomy or simply does not perform a function relevant to the species' survival. As the champion for Neuroethology, Hoy [38] points out that there is a need for nongenetic discovery science, like neuroethology, that will mine the biodiversity of neural systems and behavior mechanisms so that the *Core* Four model species will not become the *Final* Four.

As stated by August Krogh many years ago [39] and quoted by others [38, 40], "For a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied." Along the same lines, Bernard [41] stated even earlier (1865) that "In scientific investigation, the smallest processes are of the utmost importance. The happy choice of an animal, an instrument built in a certain way, the use of a reagent instead of another, are often enough to solve the highest general questions (translated from French)." In that sense, the diversity of species finds its way back into neurobiological research and our understanding of the sensory nervous system [42–44].

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Conflict of interest

The author declares that there is no conflict of interests regarding the publication of this chapter.

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