PRINCIPLES OF NEURAL SCIENCE

Fifth Edition

Edited by

ERIC R. KANDEL

JAMES H. SCHWARTZ

THOMAS M. JESSELL

STEVEN A. SIEGELBAUM

A. J. HUDSPETH

Art Editor
Sarah Mack

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Cover image: This image is a lithograph by F. Schima from a drawing by Sigmund Freud of the spinal ganglion of the lamprey *Petromyzon*. Before he discovered the unconscious, Freud had a promising career as a neural scientist. The cover thus recognizes that, a century after Freud's discovery, progress in the study of cognition has reemphasized the importance of unconscious mental processes for perception and action. (Reproduced, with permission, from Sigmund Freud, "Über Spinalganglien und Rückenmark der Petromyzon," *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, LXXVIII. Band I.

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The Autonomic Motor System and the Hypothalamus

When we are frightened our heart races, our breathing becomes rapid and shallow, our mouth becomes dry, our muscles tense, our palms become sweaty, and we may want to run. These bodily changes accompanying fear are mediated by the autonomic motor system, which controls heart muscle, smooth muscle, and exocrine glands. The autonomic motor system is controlled by a central neuronal network that includes the hypothalamus.

As we shall learn in this and the next two chapters, the hypothalamus regulates the autonomic circuits so as to recruit appropriate physiological responses for specific emotions and to coordinate these physiological and emotional responses with other aspects of behavior to insure constancy of the internal environment (homeostasis). The hypothalamus contributes to the maintenance of homeostasis by acting on three major systems: the autonomic motor system, the endocrine system, and an ill-defined neural system concerned with motivation.

The autonomic motor system is distinct from the somatic motor system, which controls skeletal muscle. Nevertheless, to produce behaviors the somatic and autonomic motor systems must work together. Whereas neurons in the somatic motor system regulate contractions of striated muscles (see Chapter 34), the autonomic motor system regulates gland cells as well as smooth and cardiac muscle, maintains constant body temperature, and controls eating, drinking, and sexual behavior.

Although the autonomic motor system is largely involuntary, the behaviors controlled by it are tightly integrated with voluntary movements controlled by the somatic motor system. Running, climbing, and lifting are voluntary actions with metabolic requirements and thermoregulatory consequences that are automatically met by the autonomic system through changes in cardiorespiratory drive, cardiac output, regional blood flow, and ventilation. Autonomic behaviors similarly are linked to emotional arousal, stress, motivation, and defensive reactions. Feelings of fear, anger, happiness, and sadness have characteristic autonomic manifestations.

In this chapter we first examine the peripheral components of the autonomic system and then their role in mediating behaviors. We then explore how these "autonomic behaviors" are orchestrated through a central autonomic network in the brain stem and hypothalamus. We conclude by considering the role of the amygdala and specialized areas of cerebral cortex in coordinating autonomic function with motivation, volition, and emotion. The autonomic and hypothalamic mechanisms involved in emotion and motivation are examined in more detail in the next two chapters.

The Autonomic Motor System Mediates Homeostasis

In the middle of the 19th century Claude Bernard in Paris drew attention to the stability of the body's internal environment, which includes the "fluid that surrounds and bathes all tissues," during a broad range of behavioral states and external conditions. Bernard wrote: "The internal environment (*le milieu interior*) is a necessary condition for a free life." Building on this idea, in the 1930s Walter B. Cannon introduced the concept of homeostasis to describe the mechanisms that maintain within a narrow physiological range the constancy of composition of the bodily fluids, body temperature, blood pressure, and other physiological variables.

As envisioned by Cannon, homeostatic mechanisms are adaptive because they extend the range of human behavior. For example, during exercise healthy people can increase their cardiac output four- to fivefold while maintaining blood pressure within a much narrower range. In the absence of these normal compensatory changes, blood pressure would increase in direct proportion to cardiac output, and the resulting increase in pressure would rupture blood vessels, perturb fluid composition, and alter the balance among the vascular, interstitial, and intracellular compartments. Increases in pressure of that proportion do not normally happen because the increase during exercise is curbed by an increase in diameter of the arteries that supply the working muscles and a resulting reduction of total vascular resistance to blood flow.

All homeostatic behavior, including control of the circulation, arises from neural modulation of the physiological properties of organ systems, mediated by hypothalamic control of the autonomic motor system and the endocrine system. We begin the discussion of these mechanisms by considering the peripheral components: the autonomic ganglia. The circuits of the ganglia connect with the spinal cord and brain stem and mediate simple reflexes that are the components of more complex behaviors.

The Autonomic System Contains Visceral Motor Neurons That Are Organized into Ganglia

Unlike the somatic motor system, in which the motor neurons are located in the ventral spinal cord and brain stem, the cell bodies of autonomic motor neurons are found in enlargements of peripheral nerves called *ganglia*.[1] The autonomic ganglia contain motor neurons that innervate the secretory epithelial cells in glands or smooth and cardiac muscle.

Overall, the nervous system has many more autonomic than somatic motor neurons. In humans the entire spinal cord contains only approximately 120,000 somatic motor nerve cells, whereas the superior cervical ganglion alone contains approximately 900,000 autonomic motor neurons. Although the significance of this difference in numbers is uncertain, it may reflect the great diversity and complexity of autonomically controlled target tissues—the stomach, intestine, bladder, heart, lungs, and vasculature—as compared to the relative uniformity of skeletal muscle controlled by the somatic motor system. Most autonomic ganglia contain far fewer cells. For example, in the lungs and gastrointestinal tract of humans there are many microscopic ganglia, each with only tens to hundreds of neurons. These differences in number of cells are thought to reflect differences in the degree of control and the size of peripheral target fields.

Efforts to understand the principles of organization of autonomic ganglia began in 1880 in England with the work of Walter Gaskell and were later continued by John N. Langley. Their pioneering studies determined how individual autonomic ganglia are functionally regulated by central nerves, and in turn how the different ganglia regulate different peripheral

[1]The peripheral nerves also have sensory ganglia, located on the dorsal roots of the spinal cord and on five of the cranial nerves: trigeminal (V), facial (VII), vestibulocochlear (VIII), glossopharyngeal (IX), and vagus (X) (see Chapter 45).