ESSENTIALS OF NEURAL SCIENCE AND BEHAVIOR

Study Guide & Practice Problems

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Front Cover: A photomicrograph of a section through the primary somatosensory cortex in the rat. Inputs originating from the thalamus have been labeled with a red florescent dye. These thalamic fibers form dense groups of synaptic terminals in layer 4 of the cortex. Each separate bundle of fibers relays information originating from a single large whisker on the animal's face, and forms the basis of an information-processing column of cortical neurons. The array of these columns forms an orderly representation of the animal's face in the cortex. Photomicrograph by Alejandro Peinado (Albert Einstein College of Medicine) and Lawrence C. Katz (Duke University Medical Center).

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Symbols

C	Capacitance (measured in farads).
C_{in}	Total input capacitance of a cell.
c_m	Capacitance per unit length of membrane cylinder.
E	Equilibrium (or Nernst) potential of an ion species, e.g., E_{Na}.
F	Faraday's constant (9.65 x 10^{-4} coulombs per mole).
G	Conductance (measured in siemens).
g	Conductance of a population of ion channels to an ion species, e.g., g_{Na}.
g_l	Resting (leakage) conductance; total conductance of a population of resting (leakage) ion channels.
I	Current (measured in amperes). The flow of charge per unit time, $\Delta Q/\Delta t$. Ohm's law, $I = V \cdot G$, states that current flowing through a conductor (G) is directly proportional to the potential difference (V) imposed across it.
I_c	Capacitive current; the current that changes the charge distribution on the lipid bilayer.
I_i	Ionic current; the resistive current that flows through ion channels.
I_l	Leakage current; the current flowing through a population of resting ion channels.
I_m	Total current crossing the cell membrane.
i	Current flowing through a single ion channel.
Q	Excess positive or negative charge on each side of a capacitor (measured in coulombs).
R	Gas constant (1.99 cal $\cdot$ K^1 $\cdot$ mol^1).

R	Resistance (measured in ohms). The reciprocal of conductance, $1/G$.
R_{in}	Total input resistance of a cell.
R_m	Specific resistance of a unit area of membrane (measured in $\Omega \cdot cm^2$).
r	Resistance of a single ion channel.
r_a	Axial resistance of the cytoplasmic core of an axon, per unit length (measured in Ω/cm).
r_m	Membrane resistance, per unit length (measured in $\Omega \cdot$ cm).
V_m	Membrane potential, $V = Q/C_{in}$ (measured in volts).
V_R	Resting membrane potential.
V_T	Threshold of membrane potential above which the neuron generates an action potential.
V_{in}	Potential on the inside of the cell membrane.
V_{out}	Potential on the outside of the cell membrane.
Z	Valence.
γ	Conductance of a single ion channel to an ion species, e.g., γ_{Na}
λ	Cell membrane length constant (typical values 0.1 – 1.0 mm).
τ	Cell membrane time constant; the product of resistance and capacitance of the membrane (typical values 1 – 20 ms).

Units of Measurement

A	Ampere, measure of electric current (SI base unit). One ampere of current represents the movement of 1 coulomb of charge per second.
Å	Ångström, measure of length (10^{-10} m, non-SI unit).
C	Coulomb, measure of quantity of electricity, electric charge (expressed in SI base units s · A).
F	Farad, measure of capacitance (expressed in SI base units $m^{-2} \cdot kg^{-1} \cdot s^{4} \cdot A^{2}$).
Hz	Hertz, measure of frequency (expressed in SI units s^{-1}).
M	Molar, measure of concentration of a solution (moles of solute per liter of solution).
mol	Mole, measure of amount of substance (SI base unit).
mol wt	Molecular weight.
S	Siemens, measure of conductance (expressed in SI base units $m^{-2} \cdot kg^{-1} \cdot s^{3} \cdot A^{2}$).
V	Volt, measure of electric potential, electromotive force (expressed in SI base units $m^{-2} \cdot kg \cdot s^{-3} \cdot A^{-1}$). One volt is the energy required to move 1 coulomb a distance of 1 meter against a force of 1 newton. Measurements in cells are in the range of millivolts (mV).
Ω	Ohm, measure of electric resistance (expressed in SI base units $m^{-2} \cdot kg \cdot s^{-3} \cdot A^{-2}$).

Preface

This workbook is intended as a companion study guide to *Essentials of Neural Science and Behavior*. The questions in the workbook follow the text closely. After completing the chapter in the textbook, students should immediately attempt the True/False Questions, Completion Problems, and Matching Problems. These are designed to reinforce key points in the textbook and do not necessarily represent typical examination questions.

The Synthetic Questions and Quantitative Problems are more in the nature of examination questions. These questions sometimes go beyond the textbook and require synthesizing ideas from more than one chapter and thinking beyond the facts. The model answers to these questions and problems should be studied carefully. Finally, some problems in the chapters that deal with cellular electrophysiology (Chapters 8 through 11) are specifically designed to give students the benefits of practical experimental work using the NeuralSim computer simulation programs provided with the textbook. NeuralSim includes two simulation programs: APSIM simulates the action potential and passive electrophysiologic properties of an axon, while PSPSIM simulates excitatory and inhibitory postsynaptic potentials.

Students who consistently use the workbook together with the textbook should find the study of neural science easier, and more rewarding.

Contents

1 & 2

Brain, Nerve Cells, and Behavior

Overview

In Chapter 1 the evidence for the localization of function in the cerebral hemispheres is reviewed by focusing on the historical development of our understanding of the neural bases of language. We have come to realize that, like all behaviors and cognitive functions, language is the product of the interaction of discrete brain areas that represent elementary neural operations and which are interconnected by serial and parallel pathways. Language function is also lateralized, being localized in the left hemisphere, which controls the right body side. The left hemisphere is considered dominant in most people as it controls the right hand, which is likewise usually dominant, as well as language. Functional specialization of different cortical areas is associated with cytological differences between these areas. Each area contains an orderly sensory or motor map of the body, depending on its function.

Modern techniques like PET scanning, which can be used to observe the physiological correlates of behavior in active human subjects, confirm the idea that different aspects of language are localized in a number of discrete areas that interact through serial and parallel pathways.

In Chapter 2 of the text the nervous system is viewed from a different perspective — from the cellular connectionist point of view. The simple monosynaptic stretch reflex is explored as a way of understanding how neuronal properties and synaptic connections form functional neural circuits that produce behavior. Cellular connectionism is based on the tenets of Ramón y Cajal, specifically the principles of dynamic polarization and connectional specificity. The first of these principles is best summed up in the words of Cajal: "Every neuron possesses a receptor apparatus, the body and dendritic propagations, an apparatus of emission, the axon, and an apparatus for distribution, the terminal arborization of the nerve fiber." (We now realize, however, that some of these elements may be missing or merged in some neurons.) The second of these principles may be summed up as follows. Neurons make specific connections with particular targets at specialized points of contact called synapses, and this specificity endows neural networks with their functional capabilities. The monosynaptic component of the stretch reflex illustrates these principles of organization and the various signals and signal transformations that neurons use to communicate.

When a muscle is stretched, activating muscle spindles, the amplitude and duration of the stretch is reflected in the graded amplitude and duration of the receptor potential in sensory neurons of the spindles. If the receptor potential exceeds the threshold for action potentials in the sensory neurons, the graded receptor potential is transformed at the neuron's trigger zone into a train of all-or-none action potentials, which continue as long as the threshold is exceeded. The larger the amplitude of the receptor potential, the higher the frequency of action potentials; likewise, the longer the duration of the receptor potential, the longer the train of action potential continues. The action potentials are conducted into the spinal cord without failure or attenuation

At the presynaptic terminals of the sensory neurons in the spinal cord, the frequency of action potentials determines the amount of transmitter released onto the postsynaptic motor neurons. The released transmitter, by interacting with postsynaptic receptors, determines the amplitude of the resulting excitatory synaptic potential(s) in the motor neuron. The graded synaptic potentials spread from the dendrites to the trigger zone at the axon hillock, and there, if they exceed threshold, they initiate action potentials. These action potentials are then conducted without failure or attenuation to the terminals of the motor neurons on the muscle. There, they initiate transmitter release and thus produce excitatory synaptic potentials in the muscle, which trigger action potentials in the muscle fibers and cause muscle contraction. Thus, a simple stimulus initiates a simple movement, the knee jerk.

Objectives

1. Understanding the historical development of our current view of the localization of function in the cerebral hemispheres.
2. Understanding the principles of cellular connectionism, illustrated by the stretch reflex.
3. Understanding the various signals and signal transformations that neurons use to communicate.

MATCHING PROBLEMS — PERSONS

1. Neuron doctrine	A. Pierre Flourens
2. Phrenology	B. Carl Wernicke
3. Aggregate field view	C. Franz Joseph Gall
4. Cellular connectionism	D. Pierre Paul Broca
5. Mass action	E. Korbinian Brodmann
6. Cytoarchitectonics	F. Camillo Golgi and Ramón y Cajal
7. Language dominance of the left cerebral hemisphere	G. Karl Lashley

MATCHING PROBLEMS — CONCEPTS

1. Receptive aphasia
2. Expressive aphasia
3. Conduction aphasia
5. Distributed processing
6. Serial and parallel processing
7. Elementary brain operations

A. Left

B. Processing of the different components of a single behavior

C. Processing in a discrete local region

E. Wernicke's area

F. Processing in all sensory and motor pathways

G. Arcuate fasciculus

COMPLETION PROBLEMS

1. There are two distinct classes of cells in the nervous system: _____________ and _____________.

2. A typical neuron has four morphologically defined regions: _____________, _____________, _____________, and _____________.

3. Most neurons have only one axon but several _____________.

4. The cell body (_____________) is the _____________ of a neuron; the dendrites serve as the site for _____________ to a neuron; the _____________ is the main conducting element of a neuron, and the _____________ are the output elements of a neuron.

5. The information conveyed by an action potential is determined not by the _____________ of the signal, but by the _____________ of the signal.

6. Many axons are surrounded by a fatty insulating sheath called ______________, which is interrupted at regular intervals at ______________, where the ______________ becomes regenerated.

7. The space between a presynaptic terminal and the postsynaptic cell is called the ______________.

8. The number of processes is a useful way of classifying neuronal types into three large groups: ______________, ______________, and ______________.

9. Neurons can be classified functionally into three groups: ______________ (or ______________), motor, and ______________.

10. Interneurons are of two types: ______________ interneurons and ______________ (or ______________) interneurons.

11. There are three main types of glial cells in the vertebrate nervous system: ______________ and ______________, which form ______________ in the central nervous system and peripheral nervous system, respectively, and ______________, which are the most numerous and have several functions.

12. The connections between sensory and motor neurons in the monosynaptic stretch reflex circuit illustrate both ______________, in which each afferent neuron synapses on several motor neurons, and ______________, in which each motor neuron receives synapses from several afferents.

13. Neurons typically produce four types of signals at different sites within the cell: an ______________ (receptive) signal, ______________ (trigger) signal, a ______________ signal, and an ______________ (secretory) signal. This functional model of the neuron embodies the principle of ______________, put forth by Ramón y Cajal.

TRUE/FALSE QUESTIONS

(If false, explain why)

1. The speed of conduction of action potentials in mammalian axons is between 0.1 and 1 m/s. _____

2. The size of axons in mammals ranges from 0.2 to 20 mm in diameter and from 0.1 mm to 2 m in length. _____

3. In most vertebrate neurons the axon hillock acts as the site where action potentials are initiated in response to synaptic inputs to the dendrites and cell body. _____

4. The neuron doctrine set forth by Ramón y Cajal holds that neurons are the basic signaling units of the nervous system and that each neuron is a discrete cell, whose several processes arise from its cell body. _____

5. The principles of dynamic polarization and of connectional specificity, while useful in the time of Ramón y Cajal, are not thought to apply to neurons and neural networks today. _____

6. Multipolar neurons predominate in the nervous systems of invertebrates. _____

7. The sensory neurons of the dorsal root ganglia of vertebrates are pseudo-unipolar. _____

8. In most neurons there is a negative correlation between the number and extent of dendrites and the number of synaptic inputs the cell receives. _____

9. There are between 10 and 50 times more neurons than glial cells in the nervous systems of vertebrates. _____

10. Glial cells are supporting elements, produce myelin, scavenge debris, buffer external K^+ ions, guide the migration of neurons during development, form the blood-brain barrier, and nourish nerve cells, but they do not participate directly in neural signaling and information processing. _____

11. In monosynaptic reflex circuits the sensory and motor neurons have one layer of interneurons interposed between them. _____

12. The afferent fiber from a stretch-sensitive muscle spindle has its cell body in a dorsal root ganglion and projects a central axon into the spinal cord. _____

13. Stretching a muscle activates several hundred sensory neurons, each of which makes synaptic contact with 100 to 150 motor neurons. _____

14. Afferent fibers from muscle spindles make synaptic contacts with projection interneurons in the spinal cord that transmit information about muscle length to higher regions in the brain. _____

15. In neurons hyperpolarization is excitatory and depolarization is inhibitory. _____

16. A reduction in the membrane potential of a neuron to a more positive value (about 10 mV) can initiate an action potential. _____

17. Receptor potentials and synaptic potentials are local signals that spread passively from their site of origin and thus attenuate sharply over a distance of 1 to 2 mm. _____

18. Receptor potentials and synaptic potentials (input signals) are graded in amplitude, but action potentials are all-or-none. _____

19. In mammals action potentials are about 100 mV in amplitude, 1 ms in duration, and travel at speeds of up to 100 m/s. _____

20. The intensity of sensation and the force and speed of movement is determined by the frequency of action potentials in a sensory or motor neuron, while the duration of sensation or movement is determined by the period of action potential production. _____

21. The message of an action potential is determined entirely by its temporal relation to other action potentials in the same pathway and not by the pathway itself. _____

22. Feedback inhibition enhances the effect of an active pathway by suppressing the activity in competing pathways. _____

23. Functional diversity among neurons results from diversity at the macromolecular level, and thus results from differences in gene expression. _____

24. Orderly synaptic connections among groups of neurons make it possible for relatively simple and uniform neuronal components of the nervous system to process complex information. _____

SYNTHETIC QUESTIONS AND QUANTITATIVE PROBLEMS

1. Identify the major areas of the left cerebral cortex involved in language.

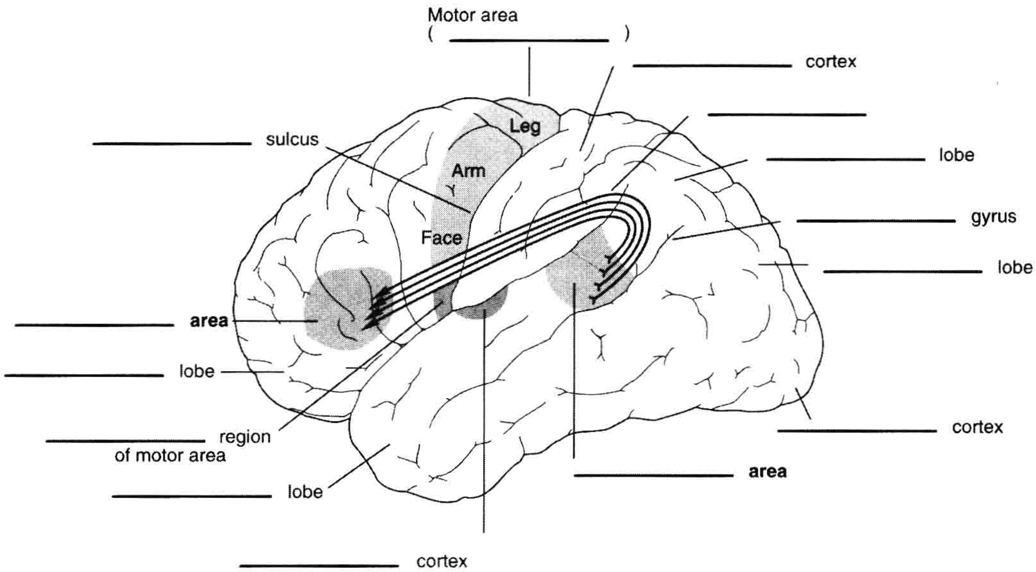

Figure 1–1

2. Identify the four signaling components of neurons and the type of signal produced by each component.

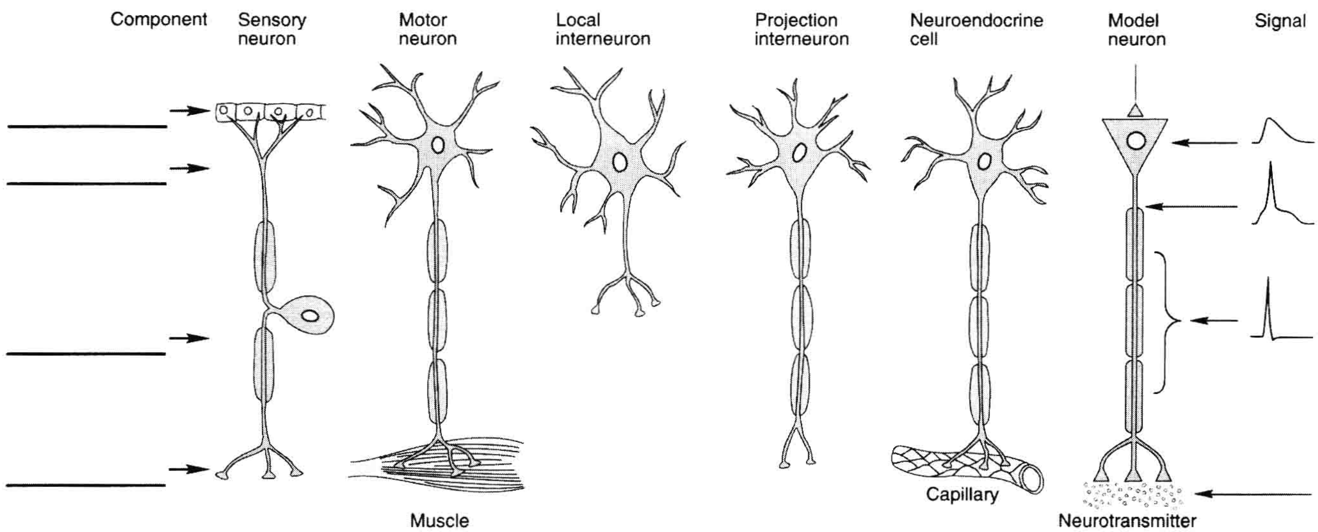

Figure 1–2