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Memory: From Mind to Molecules

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*Memory: From Mind to Molecules* represents the skillful attempt by Larry Squire and Eric Kandel to explain the cellular processes involved in the formation and consolidation of memories. Clearly written and masterfully presented, *Memory* guides the reader through complicated material step by step, such that even non-scientific readers will find the journey worth their while; those with advanced scientific backgrounds, however, will not be disappointed. As one of the first attempts to link research in the behavioral sciences with research in neurobiology, *Memory* highlights issues of interest to any reader who desires to understand the inner workings of the mind. And in the field of applied linguistics, understanding the neurobiological processes involved in learning and memory has become increasingly important.

The questions addressed by Squire and Kandel are presented in the first chapter (p.3): What is memory? How does it work? Are there different kinds of memory? Where in the brain do we learn? Where do we store what is learned as memory? Can memory storage be resolved at the level of individual nerve cells? If so, what is the nature of the molecules that underlie the various processes of memory storage? These questions shape and organize the book, with Chapters 2 and 3 dedicated to the neural architecture involved in nondeclarative and short-term memory, Chapters 4 through 7 explaining the molecular basis for declarative and long-term memory, and Chapters 8 through 10 presenting the ways in which these memory processes influence our lives on a daily basis. Throughout the book, Squire and Kandel elucidate complicated biological phenomena through stories, diagrams, and pictures of artistic masterpieces. These colorful pictures serve to remind the reader of the powerful connection between who we are and how the brain functions. In essence, the entire book is a statement of the inseparability of the fields of biology, psychology, and philosophy.

Chapter 2, which addresses the cellular mechanisms involved in nondeclarative memory, provides the first detailed look at how memory storage takes place at the level of individual nerve cells. Nondeclarative memory is the type of memory that is typically “not accessible to the conscious mind” (p.24), such as memory for motor skills (i.e., riding a bike) or habituating to a non-aversive stimulus. Though nondeclarative memory occurs subconsciously, there are clear changes at the level of individual synapses that occur as a result of learning. For example, in the first neuron to fire (the presynaptic cell) there can be an in-
crease in the number of synaptic vesicles that carry neurotransmitters used in communicating with the second neuron (the postsynaptic cell). With a higher number of vesicles, the probability that the first cell will cause the second cell to fire is much higher, meaning that performing a task will be much easier. Another change in neurons that can result from learning occurs at the structural level. In the case of habituation to a stimulus, a connection between the presynaptic cell and the postsynaptic cell might become completely ineffective, causing the processes on the presynaptic neuron to retract. This decrease in efficacy is the result of an increase in learning, for example, in a case where a person habituates, or becomes accustomed, to a loud noise or bright light not followed by any negative consequences. These basic learning mechanisms operate in accordance with the synaptic plasticity hypothesis, which states that “the ease with which an action potential in one cell excites (or inhibits) its target cell is not fixed but is plastic and modifiable” (p. 35). In other words, though most neurons are wired in a specific way at birth, the strength of the connections between these neurons can change as the result of learning.

Later chapters dealing with declarative memory present further biological and psychological descriptions of the underlying processes involved in the storage of learned experiences. Declarative memory is “memory for events, facts, words, faces, [and] music...[it is] knowledge that can potentially be declared, that is, brought to mind as a verbal proposition or as a mental image” (pp. 70-71). Chapters 4 and 5 set up Chapters 6 and 7, with Chapter 4 addressing declarative memory in terms of research in cognitive psychology and Chapter 5 introducing the brain systems involved in declarative memory. The authors’ emphasis becomes clear in Chapters 6 and 7, where the discussion is centered on the mechanisms of synaptic storage used for declarative memory and for converting learned experience into long-term memory. In these chapters Squire and Kandel discuss one of the most important and interesting phenomena in the study of learning and memory. This phenomenon, known as long-term potentiation (LTP), is now widely believed to be the major cellular mechanism for the storage of long-term memories.

LTP is an increase in synaptic strength that results from high-frequency stimulation to the presynaptic neuron. This strengthened connection between two neurons can last for hours, days, or even weeks (p.111) and involves a number of physiological changes at the cellular level. One important discovery regarding LTP is that for LTP to occur there must be changes in both the presynaptic cell and the postsynaptic cell. These changes include an increase in the release of neurotransmitters from the presynaptic neuron and a depolarization-a reduction in the membrane potential of the postsynaptic neuron.

When this happens, magnesium ions (Mg2+) that are blocking the receptors on the postsynaptic cell are expelled, opening the receptors for an influx of calcium (Ca2+). The calcium ions cause a number of chemical changes that produce a byproduct which diffuses out of the postsynaptic cell, across the gap, or cleft, between the synapses and into the presynaptic cell. Because this byproduct travels
from the postsynaptic cell to the presynaptic cell, which is the reverse direction of most synaptic communication, it has been labeled the retrograde messenger. There is now strong evidence indicating that the primary retrograde messenger involved in LTP is the gas nitric oxide (p.117).

Why is LTP believed to be the major cellular mechanism involved in learning and memory? The numerous reasons are too lengthy to discuss in detail. However, three fundamental properties of long-term potentiation have made it the primary candidate for a basic form of memory storage: associativity, cooperativity, and input-specificity. Associativity refers to the fact that both the presynaptic neuron and the postsynaptic neuron must fire in a carefully timed pairing if there is to be an enhancement of synaptic connectivity. For example, the role of the retrograde messenger is to alert the presynaptic cell that it should increase transmitter release. However, the messenger is only effective if the presynaptic neuron is already firing. In other words, for the connection between cell A and cell B to be strengthened, the two neurons must fire one right after the other. This associative property is fascinating because it is indicative of the long-held psychological understanding that two stimuli can become associated if they are paired together multiple times. The property of cooperativity refers to the cooperative involvement of multiple synaptic fibers, or afferents, involved in the firing of a neuron. This essentially means that a weak stimulation, one that fails to fire enough afferents, will not lead to the successful induction of LTP. Some researchers propose that this may be why insignificant stimuli are not remembered. Finally, the property of input-specificity suggests that in most cases only those neurons that fire during the learning experience, and not neighboring neurons, become connected.

After explaining how LTP works and why it is important, Squire and Kandel once again turn their focus to the psychological aspects of learning and memory. The final three chapters describe how priming, perceptual learning, and emotional learning occur; how skills and habits are developed; and finally, how biology can explain individuality. This final chapter is a strong reminder of the fact that humans are biological beings. Our perceptions, our actions, our philosophies, and everything about ourselves must therefore be traced to the activity of neurons in the brain. Though it is impossible to briefly review the tremendous amount of research presented by Squire and Kandel, these chapters are highly informative, presenting study after study in ways that are both interesting and enjoyable for readers with a limited scientific background.

In Memory: From Mind to Molecules, Eric Kandel and Larry Squire offer a unique view on the connection between learning and memory at the cellular level and higher cognitive processes such as our perception of the world. The authors’ bold attempt to link molecular biology to a theory of human learning and memory storage makes Memory a valuable handbook for all social scientists, including applied linguists, interested in providing a neurobiological account of psychological phenomena.
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