

Learning and memory

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Memory is one of the most fundamental mental processes. Neuroscientists study this process by using extremely diverse strategies. Two different approaches aimed at understanding learning and memory were introduced in this symposium. The first focuses on the roles played by synaptic plasticity, especially in long-term depression in the cerebellum in motor learning, and its regulatory mechanism. The second approach uses an elegant chick-quail transplantation system on defined brain regions to study how neural populations interact in development to form behaviorally important neural circuits and to elucidate neurobiological correlates of perceptual and motor predispositions.

The brain is the organ that is responsible for what we call the mind. It is the basis for thinking, feeling, wanting, perceiving, learning and memory, curiosity, and behavior. Memory is a fundamental mental process, and without memory we are capable of nothing but simple reflexes and stereotyped behaviors. Thus, learning and memory is one of the most intensively studied subjects in the field of neuroscience. Various approaches have been used to understand the mechanisms underlying this process. In this session, T.H. and E.B. presented their original approaches toward understanding learning and memory.

We define memory as a behavioral change caused by an experience, and define learning as a process for acquiring memory. According to these definitions, there are different kinds of memory. Some memories, such as those concerning events and facts, are available to our consciousness; this type of memory is called "declarative memory." However, another type of memory, called "procedural memory," is not available to consciousness. This is the memory that is needed, for example, to use a previously learned skill. We can improve our skills through practice. With training, the ability to play tennis, for example, will improve. Declarative memory and procedural memory are independent. There are patients with impaired declarative memory whose procedural memory is completely spared. Because of this fact, neuroscientists believe that there must be separate mechanisms for each type of memory that probably also require separate brain areas as well. The cerebrum and hippocampus are considered important for declarative memory, and the cerebellum for procedural memory. In any case, neuroscientists think that memory must require alterations to occur in the brain. The most popular candidate site for memory storage is the synapse, where nerve cells (neurons) communicate (1). In other words, a change in the transmission efficacy at the synapse (synaptic plasticity) has been considered to be the cause of memory. A particular pattern of synaptic usage or stimulation, called the conditioning stimulation, is believed to induce synaptic plasticity. Many questions remain to be answered, such as how synaptic plasticity is induced and how synaptic plasticity is implicated in learning and memory. Many studies concerning these issues are now in progress.

In the cerebellum, the combined activation of two different synaptic inputs to a particular neuron (called a Purkinje neuron) depresses the transmission efficacy at a synapse. This depression is persistent and is called long-term depression (LTD) (2, 3). The LTD in the cerebellum has been considered to be the cellular basis of motor learning. Hirano and colleagues succeeded in inducing cerebellar LTD in culture (4). Cellular and molecular analyses of the induction mechanism of LTD have been per-

formed with culture and slice preparations, and a number of molecules implicated in the LTD mechanism have been identified (5). A widely used strategy for identifying molecules implicated in synaptic plasticity has been to inhibit the plasticity by blocking the function of a particular molecule. These studies have relied on tools such as inhibitory drugs or on more specific molecular tools, such as antibodies.

Another frontier in the study of synaptic plasticity is to clarify the role of plasticity in learning and memory. The strategy has been to examine the correlation between synaptic plasticity and learning by inhibiting the plasticity in a living animal. To do this, investigators have used inhibitors for certain molecules that are required for synaptic plasticity. Recently, another set of very useful tools has become available. These tools are genetically engineered mutant mice such as knockout or transgenic mice. A knockout mouse is a mutant mouse that is deficient in a specific native molecule. By using mutant mice, the relationship between synaptic plasticity and learning ability has been examined (6). One model behavior that has been used to analyze the relationship between synaptic plasticity and learning is the vestibulo-ocular reflex (VOR). The VOR is the reflex that moves the eyes in the opposite direction to head motion, allowing the animal to fixate on the visual image (7). The efficacy of the VOR is modifiable and results in adjustments in its gain. For example, the gain of VOR increases if the subject wears magnifying spectacles. It has been proposed that the cerebellar LTD is implicated in such VOR adaptations. The merits of studying the VOR adaptation as a model case for motor learning are as follows. First, the neural circuit for the VOR is simple. Second, both the input (head motion) and the output (eye movement) can be quantified. Efforts are underway to analyze the relationship between the changes in neuronal activity and the VOR adaptation.

Learning does not only involve changes in synaptic efficacy resulting from the convergence of several kinds of concurrent environmental stimulation. We previously described their work on naturalistic models such as song learning in birds, suggesting that brain systems produce unlearned biases that also contribute

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Abbreviations: LTD, long-term depression; VOR, vestibulo-ocular reflex.

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