From Cells to Concepts

Review By: Norman M. Weinberger

Review of: Memory, Learning, and Higher Function: A Cellular View
By: C. D. Woody, New York: Springer-Verlag New York, 1982. 498 pp. $65.00

The neurobiological bases of learning and memory are fundamental issues in the neurosciences, and they long have been of considerable interest to behavioral scientists and workers in allied disciplines. Understanding these issues presents problems of the utmost difficulty, both because of the complexity of brains and because of the unresolved conceptual and empirical issues in behavioral neuroscience and the psychology of learning and memory. During the past five to ten years, advances in understanding the anatomy, physiology, and chemistry of neurons have yielded indications of how brains acquire and store information. This volume reviews much of the progress in cellular neurobiology related to learning. Of equal importance, it provides the challenging views of a major researcher in the field. Woody attempts to explain learning, memory, and higher function in terms of cellular processes and specific reflex brain circuits, while rejecting prior psychological approaches.

The book is divided into seven chapters, beginning with a brief consideration of commonsense views of learning. Following chapters present detailed discussions of conditioned reflexes; electrical, cellular, and subcellular events in the brain related to learning; and the role of reflex circuitry in perception, language, and conceptual processes. The book concludes with an exposition of neurocybernetics. The breadth of treatment is wide, ranging from introductory material on conditioning to the mathematics of cybernetics. Basic knowledge of cellular neurobiology and neurophysiology is required for an appreciation of the excellent discussion of subcellular processes that may be implicated in learning and memory. The book is highly documented, containing more than 1,100 references; is illustrated copiously; and has many summarizing tables and a fairly detailed index. There is a glossary that is uneven in quality and serves only as an index for many terms.

Woody's major assumptions, either stated explicitly or implied by the treatment of subject matter, include the following: (a) Knowledge is derived or can be inferred from experience; (b) the laws of causality that govern inferences are the same as those that govern the biophysical bases of brain functions on which experience and inference depend; (c) relationships between the operations of neurons and psychological functions can be established; (d) these relationships can be determined "in a formal analytic sense as in systems engineering" (p. xiv), specifically by the application of cybernetics to networks of neurons; (e) learning, memory, and higher function can be understood in terms of reflexes and reflex circuits; (f) behavioral terminology and constructs are too imprecise and anthropomorphic and are insufficiently grounded in physiology to be employed in the analytic study of learning, memory, and higher function; and (g) behavioral approaches are insufficient to investigate learning, memory, and higher function; it is also essential to investigate these processes at three levels of brain organization: the subcellular level, the cellular level, and the level of cellular networks.

The book may be viewed in more than one way and thus may be valued from more than one perspective. As a review or progress report, it is particularly strong. The chapters on conditioned reflexes are broader and more detailed than those found in many other sources. Further, Woody attempts to relate phenomena that are often considered separately, such as conditioning and pseudoconditioning. The material on neurophysiological correlates of conditioning, habituation, and sensitization provides a highly current, albeit somewhat selective, view. Woody's review of subcellular phenomena that may underlie the acquisition and storage of information is particularly cogent and comprehensive. Readers who have not been following progress in cellular neurobiology should be impressed by the number of possible mechanisms that have been delineated. The final chapter on cybernetics is a good introduction to the topic, perhaps packed a bit densely but accessible to the interested reader.
The book is not intended to be a comprehensive treatment of the neurobiology of learning, memory, and higher function, and so should not be judged on that basis. As a review and resource for selected topics, the volume should find a large audience among advanced undergraduate students, graduate students, and scientists who are interested in the neural bases of conditioning and related problems.

From another perspective, the book may be considered a proposal for the best or most appropriate way to study learning, memory, and higher function. From the viewpoint of empiricism, one may ask whether the approach advocated by Woody yields an adequate understanding of these processes. Unfortunately, this assessment will have to await future developments. However, it is possible at present to evaluate Woody's views from a conceptual standpoint.

Woody's exclusive reliance on reflexes and reflex circuits to understand not only conditioning but also higher nervous functions is traced by the author from Descartes through Sherrington, Pavlov, and Skinner: "Their insights arose from an appreciation of the fundamental significance of the reflex as a mediator of behavior" (p. 6). Because the discovery and study of reflexes originated in the field of physiology, even prior to the establishment of scientific psychology and the seminal work of Sherrington (Liddell, 1960), reflexes do satisfy Woody's argument that behavioral phenomena must have solid physiological grounding. The extension of the sensory-motor arc from the spinal cord to the brain, and ultimately to the cerebral cortex during the nineteenth century, has provided a rationale for subsequent efforts to base an understanding of learning and higher function on a reflex model (Young, 1970).

During the postwar era, Konorski's *Conditioned Reflexes and Neuron Organization* (1948) was the first major systematic attempt to explain the neural mechanism of learning on the basis of reflexes. Reflexes were later used in an attempt to explain perception, imagery, and higher function (Konorski, 1967). The present volume clearly lies within this reflex tradition, but it breaks considerable new ground. In addition to extending the approach to the cellular and subcellular levels, which were unavailable to Konorski, Woody presents a much more flexible schema. Whereas Konorski's model was based on fixed circuits, with many single neurons ("gnostic cells") identified with single percepts, Woody elaborates a much more dynamic arrangement in which single cells participate in many reflexes and many distributed neurons participate in the same reflex. The present volume does share the perspective of *Cellular Basis of Behavior* by Kandel (1976), but it transcends previous reflex formulations in scope and in its emphasis on cybernetics.

Any analysis of learning necessarily involves a particular concept of what is to be explained, that is, what is learned. One possible answer is that peripheral stimulus—response (S—R) links are learned. However, in a well-known series of classic studies, Tolman demonstrated that animals learn more than to make specific patterns of muscular contractions in the presence of a given stimulus. At least two distinctions were made: (a) learning versus performance and (b) acquisition of responses versus acquisition of information. The original Hullian S—R theory was revised to acknowledge the former but not the latter. Thus Hull and his followers still viewed learning as the acquisition of responses; however, in their final model, the S—R links were in the central nervous system.

Woody's formulation appears to renew Hullian tradition in the context of contemporary cellular neurobiology. Thus, Woody quite correctly points out that conditioned responses develop in motor neurons, and in other brain cells, many trials before conditioned responses of the muscles are elicited; consequently, purely behavioral indices of learning are inadequate to determine if learning has taken place at the time of training. This speaks to the learning—performance distinction. But to Woody, learning still consists of S—R links—within the nervous system, to be sure: "In summary, adaptive reflex operations are central to the production of memory and learned behavior" (p. 10).

Even when it is recognized that no single memory center has been found, the reflex is nonetheless invoked: "There is no single memory center, but instead, ... memory function is
parcelled out along complex reflex pathways" (p. 280). Further, Woody says that S—R links underlie higher processes as well: "The act of perceiving appears to be equivalent to the operation of the physiologic substrate relating sensory reception to motor effectuation" (p. 310); "Higher functions are supported by a number of obvious regional reflex networks" (p. 314). But the role of S—R links in higher functions is not "obvious" at all. Woody's conclusions are simply not supported by adequate data. An understanding of higher processes in terms of reflex circuits is far from clear.

However, one must be careful not to misinterpret the author. Perhaps when Woody says "reflex circuit" he sometimes means simply "circuit." But the term reflex has historically and traditionally referred to a response that is elicited fairly quickly after the presentation of a stimulus, so it is not clear what is to be gained by arguing that higher functions such as language and conceptualization are based on reflex circuits. Yet, in discussing conditioned generalization based on abstract concepts (e.g., the response to the sound of a bell generalizing to the spoken word bell), Woody concludes quite explicitly that such findings provide evidence "that there is a reflex circuitry in the dominant hemisphere of man that mediates conceptual processes" (pp. 308–309). However, no one has yet demonstrated that reflex formulations have explanatory power for understanding these processes.

One might take the view that although the reflex approach may not yet deal adequately with higher functions, it at least provides an adequate account of classical conditioning. Although there is evidence that conditioning can include learning to make specific responses following presentation of designated stimuli, it is well documented that animals also acquire and store representations that transcend S—R links, as in the case of higher order conditioning and conditioned reinforcement (for a review see, for example, Mackintosh, 1983). Woody does not recognize this side of the conditioning coin. In any event, attempts to understand even classical conditioning solely in terms of the acquisition of responses must be incomplete. Furthermore, there is ample evidence that animals invariably develop conditioned responses in several response systems during a conditioning experiment; they do not merely develop "the conditioned reflex," that is, the specific somatic reflex that the experimenter usually chooses to monitor (e.g., Schneiderman, 1972). Thus, the widespread occurrence of electrophysiological changes throughout the brain during conditioning cannot reasonably be related to a single incipient or suprathreshold behavioral conditioned response. Additionally, some of these changes in the brain are likely to involve the acquisition of information, in addition to the acquisition of S—R links. It is obviously more difficult to relate neuronal changes to the acquisition of information than to the acquisition of overt conditioned responses. The present status of knowledge in the neurophysiology of learning is more likely to reflect this state of affairs than it is to reveal verities about the neural bases of learning, memory, and higher function.

Woody's approach is thus incomplete. Shorn of its exclusive reliance on reflexes and broadened to include the need to explicitly account for the acquisition of information that transcends S—R links, it could provide a more promising avenue of inquiry into the complex problems and issues that are central to brain function and behavioral adaptation.

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