Representations in the Brain

The Hippocampus as a Cognitive Map. JOHN O'KEEFE and LYNN NADEL. Clarendon (Oxford University Press), New York, 1978. xvi, 570 pp., illus. $30.

A little more than 20 years ago Scoville and Milner reported that surgical removal of parts of the temporal lobe, and in particular the hippocampus, produced a profound memory defect in human patients. This has been one of the most (perhaps *the* most) influential observations in the history of neuropsychology, and it has launched what is now a generation of experimentation into what the hippocampus "does." Studies have proceeded at a heated pace in both the clinic and the animal laboratory, and while any number of ideas have emerged (along with a library of publications) acceptable integrative theories have seemed always distant. The book by O'Keefe and Nadel attacks the problem head on and emerges as a fascinating, erudite, and brave piece of scholarship. The authors posit that animals locate themselves in space by using cognitive "maps" and that these maps are built and stored in the hippocampal formation. Stated baldly the idea sounds simple enough, but in fact this wedding of the cognitive map with the hippocampus results in a variegated assemblage of ideas. This makes for fascinating reading but a difficult subject for brief review.

After a historical introduction to the idea of psychological space (and the degree to which it is innate), the authors get down to business and discuss the bitter arguments that once raged about how animals navigate their way through the environment: Do they chain together a series of cues and responses, or do they use an internal ("cognitive") representation ("map") of the external world? O'Keefe and Nadel find the evidence for the latter idea convincing and then proceed to investigate the properties of such maps and how they are developed.

Having made their case that cognitive spatial maps exist, even in rats, and are built and repaired according to an unusual set of rules, the authors move to the idea that such maps reside in the hippocampus. After a brief (and excellent) review of the pertinent anatomy, O'Keefe and Nadel struggle to incorporate the enormous literature on the "theta" rhythm, an electroencephalographic wave characteristic of hippocampus, into their hypothesis. I suspect that readers versed in this subject will find the arguments strained, but it hardly matters, for the authors generate their most telling points for the idea of a hippocampal map by using their own neurophysiological studies of "single unit" activity from behaving rats. They find that cells in hippocampus fall into two categories: those that discharge when the animal finds itself in a particular spot in the environment and those that fire when it encounters a strange object or the absence of an expected one. These experiments are essential to the major theory of the book and deserve an analysis that cannot be attempted in this space. The authors close the section by combining the anatomy and physiology into a model of how the hippocampus builds and uses maps. This part of the book is in many ways less satisfying than the remainder—O'Keefe and Nadel verbally wave their hands at the unit-recording studies linking the hippocampus to simple learning (that is, they resort to oddly humorless and largely rhetorical statements about the relative merits of psychology and ethology) and fail to make any real use of the exploding knowledge about the circuitry of hippocampus. Here perhaps we see one disadvantage of starting with behavior and thinking back to anatomy.

The unveiling of the model completes the first half of the book. The authors then proceed to demonstrate the power of their hypothesis by using it to analyze the extensive literature on the functional effects of hippocampal lesions. They argue that behavior after such damage reflects first a loss of the spatial map and second a reliance on a cue-specific response system. Beyond their penetrating use of the spatial hypothesis, O'Keefe and Nadel provide the reader with an eminently fair and unfailingly fresh look at the lesion literature; in fact, this part of the book is a superb textbook on animal psychology.

Finally, the book arrives at the amnesic syndrome that follows damage to the hippocampal formation in human beings, the phenomenon that has prompted so much of the research into the functions of hippocampus. The authors make use of certain recent ideas in linguistic theory and propose that the left hippocampus serves as a representational device that stores the relationships of words to each other—in short, as a semantic map. The right hippocampus according to the now-elaborated theory of a cognitive map serves to provide spatial and temporal contexts for the items to be stored. One might then think of a particular segment of the bilateral hippocampus as a "picture" of an event. Hippocampal damage according to this theory results in a loss of these pictures as well as of the ability to form new ones; it also forces the patient to rely upon simpler stimulus-response modes of information storage. So the spatial map becomes a semantic map and humans use their hippocampi to find their way through their memorial worlds in somewhat the same way rats use theirs to locate themselves in an external universe.

In this age of endless collections of symposium proceedings each like the last, this book comes as a refreshing change. What we have here is a novel, well-developed, and frankly stated theory, something that is not often seen.

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Reptilian Neuroethology

Behavior and Neurology of Lizards. An Interdisciplinary Colloquium. Poolesville, Md., and Front Royal, Va., May 1975. NEIL GREENBERG and PAUL D. MACLEAN, Eds. Alcohol, Drug Abuse, and Mental Health Administration, Rockville, Md., 1978. xii, 352 pp., illus. Paper. DHEW Publication No. (ADM) 77-491.

The biology of lizards is fascinating for many reasons. Lizard behaviors are complex, have a large number of stereotypic components, and yet are capable of modification through conditioning. As a group lizards are diverse in morphology, behavior, and ecological niche. Their brains contain structures representative of all major components of the mammalian brain, yet they lack the extensive neocortical mantle that masks the deeper structures of the mammalian brain. In addition lizards have recently proved to be particularly well suited to studies of the effects of environmental and social variables on behavioral endocrinology.

In 1975, a group of more than 20 neuroanatomists, physiologists, ethologists, psychologists, and evolutionary biologists met to share their knowledge of the structure of the brain and the behav-