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-

ior of lizards. The impetus to convening the conference was surely Paul MacLean's long-standing interest in brain evolution and behavior, and one might expect to find in the proceedings further elucidation of the triune concept of brain and behavior enunciated by him in the mid-1960's. In a simplified version the view MacLean put forth was that the human brain has a hierarchical organization of three brain types: reptilian, paleomammalian, and neomammalian. The reptilian brain, the oldest of the three, consists of the upper brainstem including reticular system, midbrain, and basal ganglia. The reptilian forebrain has, according to MacLean, only a rudimentary cortex but is characterized by expanded basal ganglia. The paleomammalian brain is characterized by an expansion of limbic cortex, and the neomammalian brain is characterized by the evolution of neocortex. In humans the three brains normally intermesh and function together in a coordinated fashion. MacLean proposed that the reptilian brain, the striatopallidal complex, is responsible for programming stereotyped behaviors based on information obtained from some form of "ancestral" learning or memories and transmitted from generation to generation. Of particular interest in this regard is the "organized expression of species-typical, communicative behavior" (p. 4).

Several testable hypotheses may be generated from this theory. For example, if the striatopallidal complex of the mammalian brain is homologous to similarly named structures of the reptilian brain, is this complex uniquely involved with stereotyped communicative behaviors in mammals? Another approach, and the one that predominates in this book, is the detailed examination of reptilian brain structure, behavioral repertoire, and brain-behavior relationships in an attempt to characterize the "reptilian brain."

As a contribution bearing on the triune concept of brain and behavior, however, the volume suffers from a paucity of correlation between brain and behavior. The first several papers deal with the structure of the central nervous system of lizards with little reference to behavior, and all but one of the remaining papers discuss lizard behavior without reference to neural mechanisms. The one paper that deals directly with brain-behavior relationships, by Hansjürgen Distel, consists primarily of an atlas of the brain of the green iguana with stimulation points charted to indicate the behavioral outcome of electrical stimulation at various loci. Interestingly, from the point of view of MacLean's theory, dewlap, defense, and head-nodding displays, the behaviors one would most closely associate with "species-typical communicative behavior," are never elicited from stimulation points in the striatal complex. Unfortunately Distel provides no discussion in his paper to guide the reader in interpreting his results.

It may be more appropriate to evaluate the volume without reference to an overriding theme or purpose but simply as a collection of reviews and research reports. As such it reflects the growth that the field of experimental comparative neuroanatomy has undergone in the last 15 years. With the advent of experimental silver staining techniques for demonstrating degenerating axons and terminals and the application of axonal transport of labeled macromolecules for identification of neural pathways in the brain, many of the early conceptions of central nervous system organization in nonmammalian vertebrates have been altered. An excellent review of our current understanding of the organization of lizard forebrains and midbrains based on these experimental techniques is provided by R. Glenn Northcutt. This review is one of the rare instances where variation in brain structures of lizards belonging to different families is dealt with in some detail. Those anatomical structures that appear to be useful as taxonomic features are discussed and contrasted to those whose variation does not follow a systematic pattern. In addition Northcutt compares the connectivity patterns of the lizards investigated with those of other reptiles and other nonmammalian vertebrates. An attempt is made, as well, to review what little is known about the functional significance of several brain structures.

Of particular interest, with respect to MacLean's concept of the striatal complex as representative of the reptilian component of the human brain, is the discussion by both Northcutt and Ann Butler of the significance of the dorsal ventricular ridge. Through several experimental examples it is now well established that areas of the dorsal ventricular ridge are targets for thalamofugal fibers related to visual, auditory, and perhaps somesthetic systems. In addition, the histochemical evidence suggests that only the more basal regions of the reptilian telencephalon are homologous to mammalian basal ganglia. Such evidence has led Northcutt, Butler, and others to conclude that the dorsal ventricular ridge may be "homologous as a field to parts of mammalian neocortex" (p. 69).

The remaining neuroanatomical papers deal with individual systems in single lizard species and include accounts of the visual system of *Tupinambus nigropunctatus* (Cruce and Cruce), the medial lemniscus of *Varanus bengalensis* (Ebbesson), and the "motor" systems of *Tupinambus nigropunctatus* (Cruce). Although not a speaker at the original conference, Philip Ulinski was asked to contribute a paper on the organization of the dorsal ventricular ridge. Though his work is based on snakes rather than lizards, his paper provides experimental data on the connections of the anterior dorsal ventricular ridge that otherwise would have been lacking in this volume.

As a group the anatomical papers are well written, excellently illustrated, and comprehensible without reference to sources outside this volume.

The second half of the book is devoted to laboratory and field studies of behavior. The major theme running through these papers relates to the ecological significance of displays used by lizards to communicate with conspecifics. Careful attention is paid by David Crews to hormonal regulation of male aggressive and courting displays in *Anolis carolinensis*. He presents convincing evidence that male aggressive behavior has an inhibiting effect on ovarian growth in females whereas male courtship behavior facilitates such growth.

Charles Carpenter presents a systematization of ritualistic display action patterns utilized in a number of lizard families. A model proposed at the end of this well-illustrated and well-documented paper suggests critical matters for future investigation.

The behavioral papers as a group make interesting reading. They vary considerably in scope, ranging from a relatively comprehensive review of acoustic behavior in lizards by Dale Marcellini to a rather restricted but no less interesting paper by Stanley and William Rand on displays and outcome of disputes occurring between female iguanas at nesting sites. To me, the most provocative paper is on the social and feeding behavior of the Komodo monitor. Walter Auffenberg describes the habitat, physical characteristics, and behavior of the monitor with sufficient detail, with the aid of excellent illustrations, to excite the fancy of any biologist.

This symposium volume, subtitled an interdisciplinary colloquium, is interdisciplinary mainly in that experts from a variety of fields were present in the same place at the same time. Not all the oral discussion is included in the volume, but it is remarkable that almost all the pub-

lished exchanges occurred between persons from similar disciplines. I hope that the symposium provided an opportunity for persons from dissimilar disciplines to meet and plan collaborative projects that will provide answers to some of the questions about the relation between brain and behavior that must occur to those who read this volume. If such collaborative efforts occur and succeed, we can look forward to major advances in our understanding of the behavioral neurobiology of lizards.

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