highly successful attempt to explain important aspects of the ocean circulation to a wide audience.

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Psychology and Neurobiology

Memory and Brain. LARRY R. SQUIRE. Oxford University Press, New York, 1987. xiv, 315 pp., illus. $24.95; paper, $14.95.

In the preface to *Memory and Brain*, Larry Squire cites the remarkable activities of the late 19th century, when Hermann Ebbinghaus, William James, Theodule Ribot, and Sergei Korsakoff provided a pioneering agenda for the study of memory in normal and brain-damaged humans. The modern era, in which the biological basis of memory is studied in laboratory animals as well as in humans, was heralded by the work of Karl Lashley and Donald Hebb in the first half of this century. Squire's book provides a contemporary view of the brain systems used for memory, with emphasis on the primate brain. Neurobiological and psychological findings are discussed in relation to the central problem of understanding memory in humans.

At the heart of this book is the theme that many fundamental questions about memory can be addressed by examining its biological organization. The scope of this endeavor is outlined in the opening chapter. An account of the organization of memory in the brain must treat the molecular events that control changes in synaptic function, the neural systems where such changes occur, and the emergence of behavioral memory from networks characterized by synaptic plasticity. Accordingly, the discussion ranges from descriptions of synaptic change, the modulation of memory by neurotransmitters and hormones, and the search for engrams to consideration of the relation of neural systems to specific features of behavioral memory. Despite its grounding in biology, the treatment is not reductionistic. Squire maintains a dialogue between the psychological and neurobiological levels of inquiry.

A fundamental question for both psychologists and neurobiologists is whether memory is a unitary entity that can be explained by a single set of general principles. The study of memory and the brain increasingly produces data that argue against this perspective. It is well known that damage in diencephalic and temporal lobe structures in humans is associated with an amnesic syndrome. Perhaps the most striking realization of the past decade or so is that these amnesic patients possess some relatively intact memory and learning capacities: when the appropriate assessment procedures are used, they can perform as well as normal subjects. Such data are obtained on tasks that require the mastery of certain motor, perceptual, or cognitive skills or that show the residual effects of exposure to items such as individual words, a phenomenon known as the repetition priming effect. Squire uses these data to emphasize the opportunity that study of the brain holds for understanding psychological processes. A naturalistic nomenclature may emerge that is based on the types of memory that can be associated with particular brain systems and thereby dissociated from one another. An important adjunct to this endeavor is the recent recognition that considerable continuity is preserved among primates in the brain systems used for memory. Nonhuman primates have been used to model the brain damage most often associated with amnesia in humans. Like amnesic patients, these animals have a profound anterograde amnesia on some tasks, along with certain preserved learning and memory capacities that, to some extent, map onto those described in humans.

The taxonomy of memory is not clearly established. It is likely that certain distinctions formulated through psychological study (for example, episodic and semantic, working and reference memory) are indeed embedded in the organization of brain systems. The properties exhibited by particular forms of memory, such as accessibility to conscious recollection, may be linked to the unique organizational and functional properties of distributed, specialized brain systems. This general theme permeates the latter half of the book.

Another quite different example of the interface between the concerns of psychology and of neurobiology is provided by the study of the nature of forgetting: the fundamental question here is whether, once established, a memory is truly susceptible to decay or simply becomes inaccessible despite its continuing representation. In a chapter entitled "Memory and the developing nervous system," Squire discusses neurobiological studies that indicate a continuous sculpting of the nervous system by the information it processes. He suggests that the issue of forgetting will be resolved ultimately by such studies of the nervous system, in which it may be determined whether synaptic changes that represent information survive or, alternatively, disappear with time or the storage of additional information.

For the younger student of memory, the book provides not only an up-to-date account of the subject but also some edifying discussions of earlier research. The evolution and demise of the concept of molecular coded information as a mechanism for memory are traced in a discussion of memory transfer experiments. A useful chapter is dedicated to a review of Wilder Penfield's work on memory localization, studied by brain stimulation during the course of neurosurgery: more recent studies that suggest a reinterpretation of these data are also discussed.

In reviewing the progress of research on memory, Squire points to an increasing interaction between psychology and neurobiology, to the mutual benefit of these disciplines. His book is clearly designed to be accessible to all parties interested in this exchange.

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Breeding Systems

Helping and Communal Breeding in Birds. Ecology and Evolution. JERRAM L. BROWN. Princeton University Press, Princeton, NJ, 1987. xviii, 354 pp., illus. $45; paper, $16.50. Monographs in Behavior and Ecology.

The evolution of communal breeding, defined in this book as breeding "characterized by the normal presence of helpers at some or all nests," is one of the most interesting and complex problems tackled by behavioral ecologists. It is interesting because helping seems to be altruistic and altruism seems contrary to the selfishness that one might expect in an evolutionary process driven by differential survival and reproduction. It is complex because hypothesized costs and benefits of helping involve virtually all the other topics in behavioral ecology (among them agonistic behavior, foraging, reproductive behavior, and cooperation), each of which involves major uncertainties. It is therefore not surprising that communal breeding has been the focus of heated debates, with researchers disagreeing over which of the potential costs and benefits drive its evolution.

In this book Brown presents a unified theoretical framework composed of the feasible alternative hypotheses about communal breeding. From this framework he identifies two major reasons for past controversies. One is failure to consider as alternative options all combinations of three key variables: dispersal, delayed breeding, and help-

ing. The other involves a failure to recognize that both direct and indirect selection (that is, effects on gene frequencies generated through effects on descendants and through effects on nondescendants) may be simultaneously influencing helping behavior in a given breeding system. Using the currently available empirical work, he evaluates the alternative explanations for the various mating systems in which helping behavior occurs. He then charts the course for future studies by pointing out areas in need of additional work and means by which such work could be conducted.

More generally, the book provides a bridge between theory, which is usually developed in terms of inclusive fitness, and empirical tests of theory, which rarely yield accurate measurements of inclusive fitness. To test theory surrogate currencies such as numbers of offspring weighted by genetic relatedness must generally be used. Brown emphasizes that when surrogates are used researchers must pay particular attention to tradeoffs such as quantity versus quality of offspring and contributions to fitness within seasons versus across seasons versus across generations.

Brown's painstaking development of his arguments and his emphasis on detail and alternatives will undoubtedly steer investigators away from oversimplified interpretations of helping behavior. His approach also indicates new directions for the study of breeding systems. Such systems may appear similar when described in terms of such traditionally invoked features as numbers of one sex bonded to members of the opposite sex; analyses of the different options associated with helping and breeding, however, indicate that the evolutionary origins and ecological interactions of such systems may be entirely different.

Brown's chapter on polyandry illustrates the diversity of conclusions that can be generated from this approach. He concludes that limited breeding habitat probably contributes to cooperative polyandrous associations in Galápagos hawks (*Buteo galapagoensis*) but that reduction in variance of food provisioning is an important factor underlying such associations in Harris's hawks (*Parabuteo unicinctus*). Abundance of food apparently favors polyandry among dunnocks (*Prunella modularis*) by allowing a female to monopolize territorial males, which then abandon territoriality within the female's home range. In the case of noisy miners (*Manorina melanocephala*) minuscule food items and a preponderance of males apparently favor a polyandry-like promiscuity, in which females use copulations to secure the future help of several males for feeding nestlings but the males violently attack each other over inseminable females.

By identifying the array of feasible explanations within traditional categories, Brown provides a focus for future investigations: to understand the diversity of these systems through a broader consideration of alternatives and experimental manipulation of key variables in natural settings.

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