BOOK REVIEWS

Non-Degenerates

Parascript. Parasites and the Language of Evolution. DANIEL R. BROOKS and DEBORAH A. McLENNAN. Smithsonian Institution Press, Washington, DC, 1993. x, 429 pp., illus. $69 or £53.75; paper, $25 or £19.50. Smithsonian Series in Comparative Evolutionary Biology.

Walter (Mike) Kemp, a former president of the American Society of Parasitologists, entitled his 1989 presidential address "Parasitology: A degenerate discipline, populated by degenerate scientists, studying degenerate organisms?" Kemp effectively refuted all three of these imputations in his address, but in the process he also showed that this common external perception of parasitology is, in large part, of our (parasitologists') own making. Parasitology has been impaired by a lack of regular interaction with other disciplines and by a failure to educate other scientists regarding what parasitology has to offer. As Daniel R. Brooks and Deborah A. McLennan point out, this has been particularly true within the subdiscipline of systematic and evolutionary parasitology. During the period from the emergence of neo-Darwinism in the 1940s until the 1970s, parasitologists usually worked outside the mainstream of modern evolutionary biology. Since that time, popular characterizations of parasite evolution have been perpetuated in textbooks but rarely examined critically by rigorous comparative methods. Brooks and McLennan suggest that because of the apparent ecological and developmental complexities of the host-parasite association, parasite evolution has commonly been viewed as a peculiar case that is poorly representative of more general processes and patterns. How did this situation come about? And perhaps more important, what can be done about it? The authors' prescription in *Parascript* calls for using characters of the parasites to infer their evolutionary history—and applying the topological information in the resulting phylogenetic trees to test competing macroevolutionary hypotheses. Throughout the work, the authors reexamine commonly held macroevolutionary theories about parasites, condense results of selected phylogenetic studies of helminths, and champion parasites as model systems for investigating questions of broad interest to evolutionary biologists. Some of these reexaminations are necessarily preliminary owing to the limited number of species-level phylogenies for parasites (and their hosts). Nevertheless, the results of these comparative studies will prove surprising to many parasitologists and most evolutionary biologists; numerous commonly accepted textbook generalizations are contradicted by phylogenetic evidence. The authors also make a strong argument for interdisciplinary studies and provide a brief overview of research areas in evolution and ecology where parasitologists can make valuable contributions.

The authors begin by providing a historical summary of how evolutionary concepts developed by parasitologists early in this century constrained subsequent advancement within the discipline. For example, parasitologists often invoked orthogenetic reasoning to explain supposed trends toward morphological degeneracy and increases in host specificity within lineages of parasites. Another subject of interest during this period was the relationship between host specificity and parasite speciation. Certain "parasitological rules" to explain host-parasite interactions were proposed on the basis of the belief that hosts were the primary determinants of parasite evolution and that both hosts and their parasites followed certain orthogenetic trends (for example, host specificity was proposed to be positively correlated with the age of the host-parasite association). One example, Fahrenholz's rule, states that the evolutionary history of parasites with high levels of host specificity will parallel the phylogeny of their hosts—and that the genealogical relationships of such parasites can be used to infer the phylogeny of their hosts. In the absence of independently derived phylogenetic hypotheses for hosts and their parasites, this assumption of widespread cospeciation sometimes led to remarkable levels of circular reasoning in host-parasite studies. Brooks and McLennan aim to remedy this overemphasis on the influence of hosts in the evolution of parasites, and they demonstrate that in certain cases host evolution and parasite evolution are largely decoupled.

Under the heading "myths, metaphors, and misconceptions," Brooks and McLennan discuss several popular principles, developed prior to the advent of modern systematic methods, that have been cited as governing parasite evolution. Some of these axioms about parasites include: (i) they are simple and degenerate when compared with free-living organisms; (ii) they are paradigms of adaptive plasticity in morphology and life history patterns; and (iii) host specificity plays a critical role in parasite speciation. Although the available data are not sufficient to reject these axioms outright, there is enough evidence to call each into question. For example, when flatworm parasites are compared to their free-living sister group to assess levels of "degeneracy" (the sister group providing the proper frame of reference for the assessment of simplification), phylogenetic analysis reveals that only about 10 percent of the character changes involve secondary losses. And within the tapeworms (the paradigm of parasite simplification), only 6 percent of the changes involve such losses. Of course, in order to determine whether these levels are low many groups of free-living organisms must first be similarly characterized.

Formulating new generalizations about parasite evolution is not the goal of the authors. Their major premise concerns *how* evolutionary questions should be investigated; "every story about parasite evolution can be investigated fruitfully (if not fully) by using the rigor of modern phylogenetic and historical ecological analysis." In some instances, the available data are too sparse to permit definitive decisions among competing hypotheses. In such cases, Brooks and McLennan use the available phylogenetic evidence as an exemplar, noting that "generalizations highlighted herein may not and need not be fundamental truths . . . their primary purpose is to serve as working hypotheses functioning as springboards for future research." Parsimony-based methodologies are the cornerstone of all comparative investigations in the book, whether the focus is parasite speciation, adaptation, biogeography, or coevolution. In fact, a book describing this methodology in somewhat greater detail—*Phylogeny, Ecology, and Behavior* (University of Chicago Press, 1991)—has also been published by the authors. Clearly, *Parascript* is not a compendium of various comparative procedures; readers interested in alternative methodologies (such as component analysis) for assessing particular areas of incongruence between trees or in statistical comparisons of tree topologies will need to look elsewhere. In general, the text should be comprehensible to non-parasitologists, although some readers may find the number of taxonomic names and technical terms challenging. Familiarity with the basic terminology of phylogenetic systematics is a prerequisite to understanding the book.

In advocating a research plan to integrate studies of parasites into the mainstream of evolutionary biology, Brooks and McLennan have challenged parasite systematists and other biologists to reconsider their assumptions about parasite biology. No doubt some of the authors' conclusions will prove controversial in certain circles, and others will be revised as more data become available. I suspect the

authors will be pleased if their conclusions are amended through the use of comparative phylogenetic methods.

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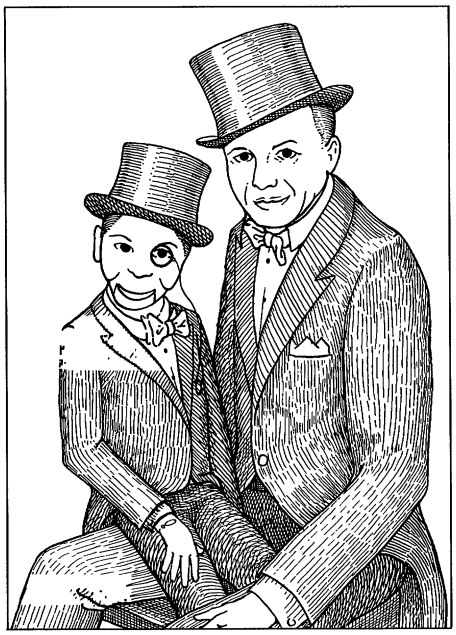
Multisensory Integration

The Merging of the Senses. BARRY E. STEIN and M. ALEX MEREDITH. MIT Press, Cambridge, MA, 1993. xvi, 211 pp., illus. $42.50 or £38.25. Cognitive Neuroscience Series.

The great majority of studies in sensory physiology have concentrated on the primary neural pathways that encode sensory information in a modality-specific way. These pathways lead from peripheral receptors that are tuned to particular forms of energy, through the brainstem and thalamus, to the cerebral cortex, where large areas are devoted to each sensory modality. Functional specialization is also observed within individual modalities. For example, functionally distinct cortical areas have been identified that are concerned primarily with the processing of specific visual features such as color or movement. At the same time, our perception of a visual scene involves the integration of those features, raising the question of how information analyzed in different regions of the cortex is linked together.

Despite the current emphasis on modality-specific processing, it is clear that integration of sensory information *across* different modalities is an essential aspect of perception. Numerous psychophysical phenomena illustrate how our perceptual experiences involve the combination and interaction of different sensory inputs. For example, our ability to understand speech is enhanced if we can observe the speaker's lips moving and thus associate the auditory and visual cues with a single source. On the other hand, if these cues are separated, as in the case of a ventriloquist's dummy, our judgments about the cues available in one modality (the speaker's voice) can be biased by the presence of conflicting cues in another (the dummy's moving lips).

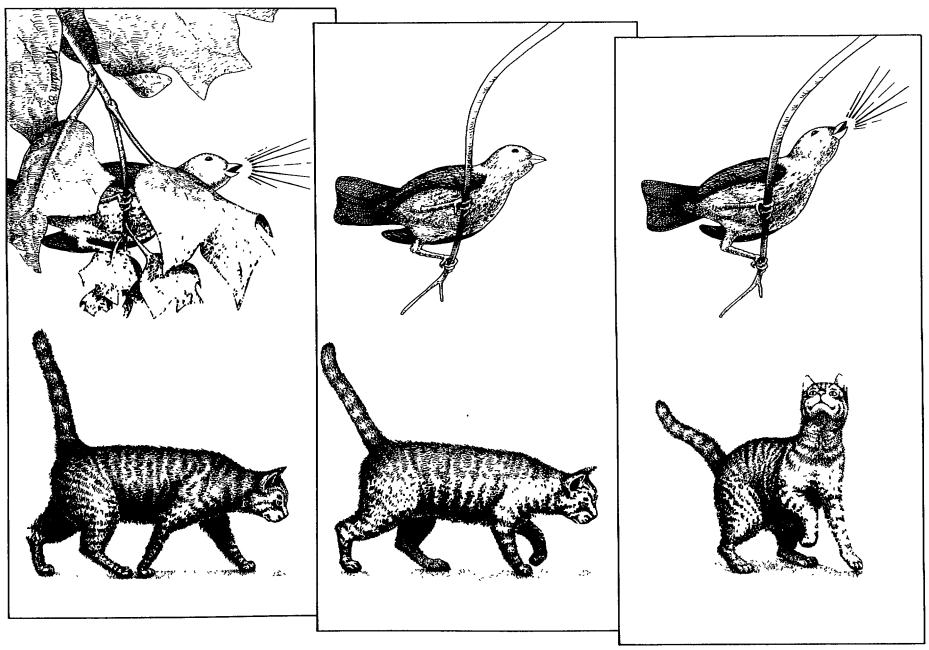
Although there is no doubting the prevalence and importance of integration of diverse sensory inputs in the construction of a coherent percept of the outside world, relatively few attempts have been made to study the possible neural basis for these effects. In fact, despite the apparently widespread distribution within the brain of neurons receiving inputs from more than one modality, it is only within the last few years that the properties of such neurons have been investigated in any detail or that efforts have been made to relate them to psychophysical or behavioral phenomena.



"The ventriloquism effect. The ventriloquist 'throws his voice' by minimizing his own movements so that the only visual cues the audience can associate with speech come from the dummy. This says less about the ventriloquist's skill than about how strong visual-auditory intersensory biases are in the audience." [From *The Merging of the Senses*]

The Merging of the Senses provides a much needed and thought-provoking synopsis of our present understanding of multisensory integration in the brain. After introducing the various cross-modal perceptual phenomena that have been described in human subjects, Stein and Meredith argue that such effects must be based on the integration of different sensory inputs at the level of the single neuron. They go on to review the ubiquity of sensory convergence at different phylogenetic levels, emphasizing the similarities found among diverse species and in different regions of the brain.

The rest of the book concentrates on the superior colliculus, which until recently was relegated by most textbooks to a purely visual role involving reflex eye movements. This midbrain nucleus now attracts the attention of a large number of sensory and motor physiologists. The superior colliculus is of particular interest for the study of multisensory integration because it contains topographically aligned visual, auditory, and somatosensory representations, and also because many of the neurons in its deeper layers receive inputs from more than one modality. Stein and Meredith first describe what is known about the sensory and motor organization of the superior colliculus and then explain how the responses of these neurons are determined by multiplicative interactions between different sensory inputs. This part of the book is dominated by experiments performed in the authors' own laboratory. Their observations suggest



"Multisensory stimuli can enhance detection and orientation behaviors. In this hypothetical situation, a bird whose song or image is within the cat's auditory (*left*) or visual (*center*) field fails to evoke an orientation response. However, when the two cues are combined (*right*), the neural activity elicited is sufficient to exceed the threshold for an overt response." [From *The Merging of the Senses*]