

Part Three

Echolocation

All the nearly 760 species of Microchiroptera have evolved sophisticated echolocation systems that they use for orientation and obtaining food. The evolution of flight and echolocation opened opportunities for a nocturnal lifestyle in largely predator-free habitats, including many unexploited food resources such as insects and arthropods, small vertebrates, blood, fruit, nectar, and pollen. These new opportunities led to extensive adaptive radiation among the Chiroptera, exhibited by an astonishing diversity. This diversity makes bats excellent models for the study of evolutionary processes.

Two components are important for understanding this extraordinary diversity in recent bats: phylogeny and environment. All these bats are related by common ancestry, but their form and function are also closely linked to the environments in which they live. If we are to understand the numerous variations in morphology, physiology, sensorimotor systems, and behavior in bats and to develop explanations for evolutionary change, we must examine both phylogenetic and environmental factors.

The principal focus of Part Three, "Echolocation," is to understand the various types of echolocation systems observed in bats. Using a comparative approach, the following

chapters examine how ecological constraints are reflected in adaptations of sensory and motor systems that are associated with echolocation. The study of echolocation systems is especially well suited for evaluating how behavioral tasks imposed by ecological constraints have led to specific adaptations. The behavioral tasks solved by echolocating bats are similar to the tasks of man-made technical systems such as sonar and radar. Thus, we can apply the theoretical framework used in the design and functional analysis of man-made systems toward understanding biological echolocation systems. When we ask how bats search for and find food, how they approach and acquire food, and how the auditory periphery of bats is adapted for echolocation, we consider the operation of biological systems in a manner similar to that in which an engineer might assess the function of a technical system designed to meet specific tasks. In other words, we infer that evolution acts as an engineer to seek the optimal solutions for specific tasks, influenced by environmental constraints (adaptations) and using the available hardware provided by biological ancestors (phylogeny).

Unfortunately, we know very little about the phylogeny of echolocation and thus the following chapters are concerned mainly with the adaptational aspect. One conclu-

sion that can be drawn from the studies presented in Part Three is that similarities in echolocation tasks are positively correlated with different echolocation systems. Thus, unrelated species subjected to similar ecological constraints have evolved rather similar echolocation systems. Many morphological, physiological, and behavioral parameters that describe echolocation systems (e.g., signal structure) are often homoplasies and cannot be used for the construction of phylogenetic trees.

Recent methodological and technical advances (sound recording and analysis, acoustical monitoring, photographic documentation, night vision devices, infrared video, and radiotelemetry) have enabled researchers to collect new information on the echolocation behavior of foraging bats in the field to address questions such as this: How do different types of habitat, foraging modes, and diet favor different kinds of echolocation systems? An important finding of comparative studies of echolocation is that the structure of search signals is intimately linked to habitat type and to foraging mode (see Schnitzler and Kalko). The signals emitted during the approach are influenced by other constraints. When approaching a target, most bats emit rather similar broadband frequency-modulated (FM) signals that permit precise localization of food or food sites. When closing in on a target, all bats reduce sound duration and pulse interval. However, maximum repetition rate differs, depending on whether the food is moving or stationary (see Kalko and Schnitzler). The high variability in signal design between and within species is another reason to be cautious when using the parameters of selected recorded signals as traits for the construction of phylogenetic trees.

Not only has the transmitter of bat echolocation systems (sound emission apparatus and echolocation signals) adapted to the ecological constraints set by different habitats, foraging mode, and diet, but also the receivers (external ear and auditory system) that process the echoes have become highly adapted. Comparative studies have demonstrated remarkable adaptations of the cochlear structure for the processing of species-specific signals, particularly in bats using long, constant-frequency (CF) signals (see Vater). Several species of bats with long CF signals adjust the frequency of sonar emissions to offset Doppler shifts introduced by their own flight velocity. A bat lowers the frequency of its sonar emissions with increased flight velocity to produce a relatively fixed echo reference frequency. This audiovocal feedback behavior is referred to as Doppler shift

compensation, and it is accompanied by high sensitivity and frequency selectivity at the echo reference frequency, which can be traced to cochlear specializations.

Species of bats that use long CF sounds are not the only ones which modify the features of their outgoing sounds in response to acoustic information carried by the echoes. Bats that use FM sonar sounds also adjust the duration, repetition rate, and bandwidth of their vocal signals with changing echo information. The sensorimotor feedback system of FM bats, which has been studied in behavioral and neurophysiological experiments (as shown by Valentine and Moss), depends on a three-dimensional system of coordinates for tracking sonar targets. Bats estimate the horizontal position of a target from interaural differences in echoes, the vertical position from spectral filtering by the external ear, and target distance from the time delay between the outgoing sound and the returning echo. It is the time delay between the sonar emission and the echo that guides range-dependent vocal behavior in bats. The neural mechanisms that support information on target-distance processing in the bat have been studied in extracellular recording experiments, and it has been postulated that single cells which show the response characteristic of echo-delay tuning may play a role in guiding range-related behaviors in bats (see Valentine and Moss; Dear). However, discrimination of target distance by FM bats that perform in laboratory experiments suggests that animals can detect changes in echo delay which are several orders of magnitude smaller than the width of the sharpest echo-delay tuning curves measured for single neurons. This discrepancy between behavioral performance and neurophysiological data challenges us to explore other characteristics of neural response that may support range processing in the central nervous system of bats (see Dear).

The echolocation system of bats has been studied extensively in the field and the laboratory. Field research permits a detailed analysis of an animal's natural sonar behavior. Laboratory research emphasizes the experimental study of echolocation and includes studies using behavioral, neurophysiological, and neuroanatomical methods. Each line of research complements the other, and representative work on echolocation in bats using these different approaches provides a glimpse of the constraints under which echolocation systems have evolved.

HANS-ULRICH SCHNITZLER AND CYNTHIA F. MOSS