Chapter 17
The Auditory Midbrain in Bats and Birds

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1. Introduction

1.1. Evolution and Phylogeny

Both bats and birds are flying vertebrates that diverged early in evolution. Their flight mechanisms are different, and so are their auditory systems. They share a common ancestor in the Carboniferous era, but their auditory systems evolved in parallel and are not homologous (Clack 1997). However, other ancestral mammalian traits, such as moveable ears, multiple ossicles, and echolocation have modified the ear and the auditory system of bats. We discuss both species because they reveal neuroethological principles that relate neural activity to behavior.

1.2. Behavioral Context

Bats and birds use hearing to localize and analyze sound sources passively, and to communicate with conspecifics (Kanwal et al. 1993; Konishi 2000). Some birds learn song and have forebrain areas to control vocal pathways. Others, like the barn owl, are nocturnal predators with superb sound localization skills. Bats use their extraordinary hearing in concert with stereotyped vocalizations and listen to the echoes from objects. By analyzing how echoes have been modified from the original sound by reflective objects, bats perceive obstacles and capture flying insects in darkness.

1.2.1. Bat Hearing and Echolocation

Bats are Chiroptera, an order closely related to insectivores. Because bats use their sense of hearing to perform tasks that in other mammals are guided by vision, their auditory system has undergone a corresponding species-specific hypertrophy and specialization (Neuweiler 1990). The inferior colliculus (IC) is a structure critical for hearing that has evolved to fulfill unique functional needs for different species of bats.
There are approximately 1000 bat species and each uses a different pattern of vocalization for echolocation (Neuweiler 2000). Bats that hunt for insects in open spaces (e.g., the Mexican free-tailed bat, *Tadarida brasiliensis*) use short-duration frequency-modulated (FM) calls. Bats that hunt in foliage use calls with a long constant-frequency (CF) component and a short FM component (CF-FM calls). The best studied CF-FM species are the mustached bat, *Pteronotus parnellii*, and the horseshoe bats, *Rhinolophus rouxi* and *R. ferrumequinum*. Other species, like the big brown bat, *Eptesicus fuscus*, use either CF- or FM-type calls (Fig. 17.1) depending on circumstances (Simmons 1989; Grinnell 1995).

Bat echolocation calls are modified in predictable ways by objects. The interval between call and echo is proportional to the distance of the reflective object. The attenuation of the echo depends on the object’s size and distance. Three-dimensional structures create characteristic interference patterns in the echoes (Simmons 1989). The IC contains neurons sensitive to all these features of echolocation signals.

All bat species listen to sounds passively and most echolocate. Species that glean from surfaces such as the pallid bat, *Antrozous pallidus*, listen to sounds made by prey (Fuzessery et al. 1993). Many bat species have a rich repertoire of communication sounds that differ from echolocation calls in temporal structure (Kanwal et al. 1993).

Because there is so much information on the patterns of sound that are behaviorally relevant, bats have become an important model system in which to study temporal aspects of sound processing. Although bats are specialized mammals, much of what has been learned about their auditory systems can be generalized to other mammals (Covey 2003).

1.2.2. Avian Hearing

Psychophysical tests have measured auditory sensitivity, loudness, and temporal resolving power in several species of birds. These data resemble those for other vertebrates, including humans (Dooling et al. 2000). Birdsong has become a model for complex sound processing, especially in the auditory midbrain (Theunissen et al. 2000). Studies of the owl, a sound-localization specialist, have implications for spatial hearing, while the development of the map of auditory space has become a paradigm for studies of experience-dependent plasticity (Knudsen 2002).

1.2.3. The Auditory Midbrain: A Hub of the Central Auditory System

In birds and mammals, the midbrain occupies a central position in the auditory system, receiving input from many ascending and descending sensory pathways as well as motor and modulatory projections. The IC projects to the thalamus and has abundant motor and premotor targets (Covey and Casseday 1995; Carr and Code 2000). Besides developing selectivity for biologically relevant sounds, the IC likely transforms the high rate of auditory input into a slower rate of