Introduction

Echolocating animals transmit sonar signals and use information contained in the returning echoes to determine the position, size, and other features of objects. This active system allows echolocating bats and dolphins to forage, avoid obstacles, and orient in the absence of light. Since echolocating animals probe the environment with the acoustic signals that drive behavior, detailed studies of sound production and feedback control are central to understanding the process of echolocation. This chapter reviews studies of sonar signal production and feedback control in echolocating bats.

Acoustically Guided Behavior in Echolocating Bats

Field and laboratory studies of foraging behavior in bats reveal a host of adaptive motor responses to dynamic acoustic input from sonar echoes (e.g., Griffin 1958). These adaptive behaviors include changes in the aim of the bat’s head and external ears, the direction of the flight path, and the features of the sonar signals. The aim accuracy of the bat’s head is approximately 1–2°, and adjustments in the flight path are both rapid and agile (Webster 1963a, 1963b; Wilson and Moss, chapter 3, this volume). As a bat flies toward an insect target, the features of the sonar vocalizations change (see fig. 1.1), contributing to a complex set of adaptive behaviors in response to dynamic acoustic information (Griffin 1958).

Sonar signal production determines the acoustic energy that drives the animal’s behavior. That is, the timing, frequency content, and duration of sonar signals used to ensonify the environment directly influence the information available to the bat’s acoustic imaging system. In turn, the bat’s perception of the environment that builds upon information contained in sonar echoes influences the bat’s motor behaviors, including vocal control. By detailing the features of the bat’s vocal behavior that enter into this audiomotor feedback system, we develop a better understanding of the underlying neural and perceptual processes.

Adaptive vocal behavior exhibited by bats falls broadly into two categories: velocity-dependent adjustments in sound frequency and range-dependent adjustments in sound duration, bandwidth, and repetition rate. Adjustments in sound frequency are most salient in species of CF-FM bats, and adjustments in sound duration and repetition rate are most salient in FM bats; however, CF-FM bats also show changes in temporal patterning with closing target distance, and FM bats show changes in the bandwidth of their signals during target approach (Schnitzler and Henson 1980). Details of adaptive vocal behaviors are discussed below.

CF-FM Bats

As a bat flies toward a target, its relative velocity introduces Doppler shifts in the returning echoes. Some species of CF-FM bats lower the frequency of their sonar vocalizations to compensate for echo Doppler shifts, receiving echoes at a relatively constant reference frequency (see fig. 1.2: Schnitzler 1968; Schuller, Beuter, and Rübsamen 1975). The CF-FM bat’s Doppler-shift compensation thus serves to cancel echo frequency shifts due to its own flight velocity and isolates Doppler shifts in echoes that come from fluttering insect prey. Laboratory experiments demonstrated that CF-FM bats do not

Fig. 1.1. Spectrograms of sonar signals produced by four different bat species as they advance from the search to approach and finally to the terminal phase of insect pursuit. Note that signal duration decreases and repetition rate increases as the bat gets closer to contact with the insect prey. (Adapted from Simmons, Fenton, and O’Farrell 1979.)
compensate for Doppler shifts that arise from fast movement of single targets (e.g., insect prey) in the bat's environment (e.g., von der Emde and Menne 1989).

Doppler-shift compensation first was discovered in the greater horseshoe bat, *Rhinolophus ferrumequinum* (Schnitzler 1968), a species that uses CF-FM signals up to more than 100 ms in duration. This behavior has been demonstrated also in other species, like *Pteronotus p. parnellii* (Schnitzler 1970) and in hipposiderid bats (Habersetzer, Schuller, and Neuweiler 1984). Accuracy and consistency of compensation performance are different among species.

The echo reference frequency to which bats compensate is species-specific and characteristic for each individual (e.g., approximately 83 kHz in *R. ferrumequinum* (Neuweiler, Bruns, and Schuller 1980). The auditory systems of Doppler-shift compensating bats are highly specialized in the relevant frequency range for fine frequency analysis (e.g., *R. ferrumequinum* can detect frequency shifts as small as 30–60 Hz, Schnitzler and Flieger 1983). Details of auditory specialization for Doppler-shift compensation are described elsewhere in this volume. The co-evolution of echolocation sound production and auditory system in Doppler-compensa-
FM Bats

In FM bats, the most notable changes in sonar vocalizations occur with a reduction in target range. The FM bat increases the signal repetition rate, decreases the signal duration, and modifies the signal bandwidth as it approaches a sonar target (Webster 1963a, 1963b). Similar to the CF-FM bat, the FM bat’s echolocation behavior depends on an audio-vocal feedback system, but the most dramatic changes in vocalizations occur with a reduction in target echo delay, rather than with changes in relative velocity. Each frequency in the FM sound provides a marker for arrival time (Moss and Schnitzler 1989). Bats that use broadband FM signals are well suited to detect small changes in echo delay, which is the bat’s cue for target distance (Simmons 1973). Indeed, one FM bat species, Eptesicus fuscus, detects differences in echo arrival time smaller than 0.5 μs, corresponding to differences in target range less than 0.1 mm (Moss and Schnitzler 1989; Simmons, Moss, and Ferragamo 1990).

Vocalization in the Developing Bat

The development of vocal signals has been studied in bats of several different families, including Vespertilionidae (e.g., Antrozous pallidus) by Brown, Grinnell, and Harrison 1978; E. fuscus and Myotis lucifugus by Gould 1971; Nycticeius humeralis by Scherrer and Wilkinson 1993; Pipistrellus pipistrellus by Jones, Hughes, and Rayner 1991; Molossidae (Tadarida brasiliensis) by Gelend and McCracken 1986; Nocotilloidae (Nocitillo albiventris) by Brown, and Grinnell 1983; Phyllostomidae (Phyllostomus discolor) by Esser and Schmidt 1989; Rhinolophidae (R. ferrumequinum) by Konstantinov and Makarov 1987; R. ferrumequinum Nippon by Matsumara 1979; Rhinolophus rouxi by Rübsamen 1987; and Hipposideridae (Hipposideros speoris) by Habersetzer and Marimuthu 1986. In the early postnatal period, the vocal repertoire of an infant bat differs from that of an adult (Brown and Grinnell 1980). During postnatal development, a bat’s vocalizations rise in frequency, decrease in duration, and become increasingly stereotyped (e.g., Gould 1971; Konstantinov and Makarov 1987; Matsumura 1979; Brown, Brown, and Grinnell 1983; Habersetzer and Marimuthu 1986; Rübsamen 1987; Moss 1988; Jones, Hughes, and Rayner 1991). See, for example, fig. 1.3.

The ontogenetic changes in frequency, bandwidth, sweep rate, and duration of the sounds produced by bats can reflect maturation of the larynx, its muscles and its innervation (Gould 1975). Maturation of the respiratory organs and their coordination with vocal organ musculature, along with the development of central motor circuits controlling vocalizations, also are important to the ontogeny of sonar signal production in bats; however, the relative contribution of each has not been studied developmentally.

The change in vocalization frequency occurs with an ontogenetic increase in auditory responses to high-frequency sounds (e.g., Konstantinov 1973; Brown, Grinnell, and Harrison 1978; Rübsamen 1987; Rübsamen, Neuweiler, and Marimuthu 1989). Developmental data on auditory function in young bats come from neurophysiological measures, typically pure-tone evoked responses from the inferior colliculus in anesthetized animals; auditory evoked responses from several bat species show that the onset of hearing generally occurs by the second postnatal week (Konstantinov 1973; Brown, Grinnell, and Harrison 1978; Rübsamen 1987). Neurophysiological data indicate that the bat’s auditory system develops to process the ultrasound frequencies present in the adult echolocation signal; however, they do not provide direct measures of echo information processing during development.

Research on developing horseshoe bats demonstrates that early deafening (three to five weeks) affects the constant-frequency (CF) component of the echolocation pulses (Rübsamen 1987). The frequency shifted by between +4 kHz and −14 kHz from preoperative conditions, and the intensity of the first and third harmonics increased considerably. The latter is due to a mismatch of vocal production and filter characteristics of the supralaryngeal filter. While disruption of auditory feedback markedly influenced the development of the normal “adult” vocal frequency pattern, the prevention of
normal vocalization by cutting the laryngeal nerves had no influence on the normal development of cochlear tuning and the responses of the auditory system. The control of echolocation pulses seems to be under auditory feedback control throughout postnatal development, whereas maturation of the auditory periphery and its frequency tuning appear to be innate processes.

Vocal Control

Sound Production

The peripheral vocal apparatus of the bat is a "basic" mammalian larynx, and the mechanisms for the production of calls are essentially the same as those found in other mammals. The spectral composition and the temporal structure of the bat's vocal signals are determined largely at the level of the larynx. The supralaryngeal transmission pathway has relatively fixed filtering properties that allow only moderate modulations of the spectral content of the vocalizations. Some bat species emit vocalizations through the nostrils, and the morphology of the transmission pathway determines the transmission filter characteristics. Modulation of the emitted calls in nose-leaf vocalizers therefore is more restricted than in open-mouth vocalizers. As described above, the duration of echolocation calls spans from very short (fractions of milliseconds) to comparatively long (several tens of milliseconds). In bats using FM calls that sweep through an octave in only a few milliseconds, the laryngeal musculature controlling sound frequency must deploy its activity in very short periods. In bats using long CF-FM signals, the emitted constant-frequency component is maintained for tens of milliseconds, immediately followed by a rapid modulation of frequency. The spectral composition of these signals requires very fast and precise neural control over the laryngeal musculature controlling frequency. The fundamental glottal pulse frequencies produced by bats generally are high in comparison to other mammals.

In addition, the repetition rate of vocalizations ranges from 5 to almost 200 sounds per second. At slow sound production rates, the bat typically emits a single vocalization for each expiratory cycle. At higher rates, the bat's vocalizations are toggled on and off within milliseconds, resulting in a burst of calls during a single expiration. Concurrent with sonar signal production is the contraction of middle-ear muscles that temporarily influences hearing sensitivity (Jen, Ostwald, and Suga 1978).

The dynamic control of vocal parameters in bats requires a laryngeal apparatus that produces high-frequency signals with very rapid spectral and sound pressure changes in the range of milliseconds. Of the many chiropteran species, the larynx has been studied in detail in only a few (Fischer and Gerkens 1961; Griffiths 1983; Denny 1976). For a review of sound-production mechanisms in bats, see Suthers 1988.

It should be emphasized that there is no typical "bat larynx," but that different species show modifications of a basic mammalian plan (see fig. 1.4). The size of the bat larynges relative to body size generally is large compared to other mammals. In most bat species that emit echolocation pulses through the nostrils, the larynx fits into the nasal part of the pharynx, thus separating the trachea and the mouth mechanically (Denny 1976), which allows for feeding and vocalizing in parallel. Generally, the supraglottal tube is short in bats, and the epiglottis is in contact with the palate or within the nasopharynx. This is also the case in some other mammals, but not in humans.

In many bat species, the laryngeal cartilage (thyroid, cricoid, and arytenoid) shows ossification at an early age. Calcification and ossification in the human larynx do not typically occur before the third decade and are considered to be degenerative processes. The ossification of laryngeal cartilage found in bats probably provides rigid scaffolding for spanning the strongly developed intrinsic laryngeal musculature. Ossification is different among species: early ossification appears in Rhinolophidae and Emballonuridae, but it is less common in Phyllostomidae (Denny 1976); usually it is limited to locations where muscles are attached.

The combination of aerial living and echolocation demands high metabolic consumption, along with high respiratory activity for flight and high laryngeal activity for vocal production. Vocalization occurs principally with an increase of resistance in the respiratory tract. The need to breathe and vocalize at the same time resulted in glottic modifications in bats. Enlargements in the region of the posterior commissure in the glottis permits respiration during adduction of the cords, and thus vocalization takes place during effective expiration (Denny 1976). Whether the large tracheal air sacs in bats, which emit long constant-frequency sonar signals, play some essential role within this context or serve different purposes remains a matter of discussion (Suthers 1988).

Innervation

The intrinsic laryngeal musculature is innervated by two laryngeal nerve branches, the recurrent (or inferior) laryngeal nerve and the superior laryngeal nerve. Both have their somata in the nucleus ambiguus (NA), located in the medulla oblongata. The recurrent laryngeal nerve ipsilaterally contacts all muscles except the cricothyroid muscle, for which motor innervation originates exclusively from the external branch of the superior laryngeal nerve. The only bilaterally supplied muscle (through the recurrent laryngeal nerve) is the inter-arytenoid muscle, the relaxation of which leads to adduction of the vocal folds. Bilateral, but not unilateral, denervation of the recurrent laryngeal nerves resulted in suffocation of the horseshoe bat, perhaps due to bilateral innervation of the inter-arytenoid muscle (Schuller and Suga 1976).
In addition, the branches of the laryngeal nerves also have vaso- and secretomotor fibers of vegetative origin that carry sensory information from laryngeal tissue to the central nervous system. Both aspects have drawn little attention for study in the bat. The laryngeal nerve supply in mammals is not uniform, but several types of nerve communications between recurrent and superior laryngeal nerve branches have been described. The reported patterns range from no connection between the two nerves to various communicating patterns between the recurrent branch and the interior superior branch. Two species of Chiroptera have been investigated in this respect and showed the pattern of complete separation of the nerve branches (Bowden 1974).

**Comparison of Final Common Pathway for Vocalization in Bats with Other Mammals**

As noted above, somata of the laryngeal nerve fibers are located in the nucleus ambiguous (NA), a rostrocaudally elongated structure in the medulla oblongata. Nerve transactions show the functional involvement of the superior laryngeal nerve in the control of vocal frequency, as well as the importance of the recurrent laryngeal nerve for the temporal control of call production (Rübsamen and Schuller 1981). Tracer experiments revealed a partial topographic separation of motoneuron pools in the NA, with superior laryngeal nerve motoneurons represented more rostrally and recurrent laryngeal nerve motoneurons located more caudally (Schweizer, Rübsamen, and Rühle 1986; Kobler 1983). This organization in bats compares well with that in other mammals.

The control of laryngeal muscles is only one of many preconditions for vocal production, and it must be coordinated with the control of respiratory and pharyngeal muscular activity (see fig. 1.5. Lancaster, Henson, and Keating 1995). Holstege (1989) proposed a final common pathway for vocalizations in mammals, coordinated by activity in the nucleus retroambigualis that lies caudal to the NA. His neuroanatomical investigations in
the cat showed that the retroambigual nucleus has connections to respiratory centers and the NA as a vocal motoneuron pool, and it receives input from the lateral periaqueductal gray (PAG) and adjacent tegmental areas (Holstege 1989). In the rat, cat, and monkey, the PAG is considered the most important relay station for the control of vocalizations in the midbrain. Stimulation in the PAG evokes vocalizations (Jürgens 1994), while bilateral lesion of this region leads to mutism. Stimulation in the PAG and the adjacent tegmental areas in bats also evokes emission of vocalizations (see fig. 1.6; Suga et al. 1973; Schuller and Radtke-Schuller 1990). However, the electrical current levels required to elicit vocalizations from the PAG in bats is higher than several distinct, highly specific low-threshold areas in more lateral regions of the mesencephalon. Furthermore, there are differences in the vocal signals elicited by microstimulation of the PAG and other low-threshold vocal motor structures (see below).

Differences in the stimulation paradigms and in the conditions for eliciting vocal responses at different sites are important and must be considered carefully. In bats, short bursts of electrical pulses lasting up to some tens of ms at vocalization-specific sites (midbrain, not PAG) induce single calls or short (two to five) series of calls. The latency is well defined and short (several tens of ms) and the stimulation-response ratio is clearly one-to-one. In the nonchiropteran mammals, stimulation in the PAG commonly consisted of a series of electrical pulses at a given frequency, lasting for several seconds that provoked prolonged call sequences. Thus, in the latter case, the stimulation appears to induce vocal behavior in the animal in a more general sense and not with a distinct one-to-one relationship of stimulus and vocal response. In general, the indicated threshold currents (peak current applied) for eliciting vocalizations in the PAG and adjacent tegmental regions are higher than in vocalization-specific areas in the bat (by a factor of about three).

Several questions, therefore, arise in the context of electrical stimulation for eliciting vocalizations. Are the mechanisms to evoke vocal responses in the PAG and other vocalization-specific sites in the midbrain functionally different? Are the stimulation sites part of different systems influencing the vocal behavior? Can the pathway originating from the PAG, as determined by limbic influences, be distinguished from a pathway that sets predominantly the physical preconditions of vocal response?

To date, answers to these questions are inconclusive. It seems, however, that a hierarchical organization of the vocalization pathway leading from the PAG to the retroambigual nucleus, as proposed for other mammals, does not adequately describe the complexity of the descending vocalization system at the brainstem level in echolocating bats. The connections from the PAG to the NA have been established in the bat, using retrograde marking after tracer injections (horseradish peroxidase, or HRP) in the NA (Rübsamen and Schweizer 1986). However, the only explicit demonstration of a connection targeting the NA proper was from the cuneiform nucleus with WGA-HRP injection in this nucleus after functional identification via electrical stimulation (Schuller and Radtke-Schuller 1988). The study of bats lacks conclusive demonstrations of vocal connections reaching the NA and more caudal structures immediately adjacent to the NA. To date, there has been no demonstration of a separable retroambigual structure in the bat. It is therefore unclear whether a final common pathway controlling vocalizations in the bat is organized similarly.
to other mammals. Therefore, tracing of the connections with the NA and adjacent regions using reciprocal tracer methods and concurrent physiological measures of the vocal relevance of these connections is needed.

Control Levels Converging on the Final Common Pathway for Vocalization: Respiratory Control and Vocalization

Vocalizations in bats are linked closely to respiratory activity and other motor behaviors, such as pinna movements, wing beats, or middle-ear muscle contraction (Jen, Ostwald, and Suga 1978; Lancaster 1994; Valentine, Sinha, and Moss in press; Wilson and Moss, chapter 3, this volume). These motor activities are controlled and coordinated precisely. The neural pathways involved in coordinating respiration, vocalization, middle-ear muscle contraction, pinna movements, and wing beats have not been investigated in the bat in detail. Only piecemeal information form parts of this puzzle.

Temporal structuring of outgoing vocalizations depends predominantly on the activation of laryngeal muscles in precise temporal coordination with expiration. The recurrent laryngeal nerve, which innervates all laryngeal muscles except the cricothyroid muscle, is the main laryngeal afferent involved in the timing of vocalizations (Schuller and Suga 1976; Rübsamen and Schuller 1981). The motoneurons of the recurrent laryngeal nerve are found predominantly in the caudal portions of the NA (Schweizer, Rübsamen, and Rühle 1986). There are some indications in the greater horseshoe bat that different portions of the NA are connected differentially to structures involved in the control of respiration; however, the functional connection of subdivisions of the NA has not been studied in detail (Rübsamen and Schweizer 1986). Neurophysiological measurements in the horseshoe bat revealed neurons that are exclusively active during a particular phase of respiration were found, as well as neurons that are exclusively active during vocalization and silent during expiration. Researchers also identified a class of neurons that are active during both respiration and vocalization, but no clear topographical arrangement could be determined (Rübsamen and Betz 1986; Rübsamen and Schweizer 1986).

The intensity of vocalization is not a parameter determined by laryngeal control exclusively, but it demonstrates most impressively how a vocal parameter is determined by expiratory control. The building of subglottic pressure and thus the availability of respiratory volume determines the vocal intensity over long calls or during bursts of multiple vocalizations (e.g., final buzz). It is unknown whether and where there is a unique structure providing the final common pathway for vocalization in the bat, as in the cat or monkey (Holstege 1989). This topic is addressed in following sections.

General Vocal-Motor System

Motoneurons controlling the laryngeal and respiratory musculature are modulated by premotor interneurons in the brainstem that receive input from various sources. Terminal areas project to the trigeminal, facial, hypoglossal, and ambiguous nuclei, whereas premotor neurons projecting to respiratory motor centers are located in the medulla. In the cat, the rat, and the monkey, the nucleus retroambigualis, an area posterior to the NA, plays a coordinating role as center of the common final pathway, just before the control level of the laryngeal and respiratory motoneurons for the vocalization pathway (Holstege 1989). In the bat, this portion of the reticular formation surrounding the NA caudally has neither been distinguished cytoarchitectonically or its afferent connections established differentially. The afferent and efferent connections to the NA has, however, been studied extensively in two bat species: the horseshoe bat (Rübsamen and Schweizer 1986) and the mustached bat (Kobler 1983).

A number of brainstem areas potentially project to the region of the NA; however, the relevance of these afferent projections to the NA for vocal control has been studied in only a few sites. In the horseshoe bat, retrograde labeling from the NA was found in very lateral portions of the PAG and the adjacent tegmentum, the cuneiform nucleus. Tracer injections centered in the cuneiform nucleus, but possibly encroaching the lateral PAG, yield anterograd labeling in the NA. There have not been tracer injections into the PAG proper in this bat species yet, so the connection from the PAG has not been explicitly shown and could result from tracer uptake by fibers of passage in the NA. In the mustached bat, the connection from the PAG to NA was shown by retrograde labeling concentrated to the medial divisions (adjacent to the aqueduct) and not encroaching to the lateral adjacent tegmental regions (Kobler 1983). There is no reciprocal demonstration of this connection in this bat species. The sparse knowledge on the afferent projections to NA in the two species, besides being partly contradictory, shows that the NA neurons receive potentially modulatory input from tegmental or periaqueductal regions, which are not mediated by a retroambigual area (see fig. 1.7).

In monkeys, the PAG constitutes the most important brain center for vocal coordination. This was demonstrated in numerous reports (Jürgens 1994) that showed that the influence of anterior structures on vocal utterances are obligatorily mediated by the PAG. Electrical stimulation of PAG subdivisions further supports the notion that there exists a local differentiation with respect to different communication call structures.

The involvement of PAG in vocal control has not been demonstrated in the bat as conclusively as in the monkey. Electrical stimulation in the periaqueductal re-
gion elicited vocalizations in bats (Suga et al. 1973), although it is not clear how much the laterally adjacent tegmental structures were involved in the vocal activation in these studies.

Electrical stimulation in the lateral regions of the PAG and the cuneiform nucleus in the horseshoe bat elicits vocalizations (Schuller and Radtke-Schuller 1990). However, electrical stimulation in these structures always elicits general arousal or body movements after short periods of current delivery. The latency of the response is long and less consistent compared to stimulation in other vocally responsive regions of the midbrain (e.g., the paralemniscal area). This clearly indicates a functional involvement of these two regions in vocal control. On the other hand, the nonvocal reactions further suggest their involvement in the motivational control of vocalizations.

The PAG constitutes a part of the descending vocal pathway and receives input from limbic structures that presumably play a role in emotional behavior. An important afferent connection originates in the anterior part of the cingulate cortex and was demonstrated in the bat as a functionally important structure for vocalization. Electrical stimulation of this site in the limbic cortex induces vocalizations with relatively long latencies: the locus of stimulation determines the frequency of the onset of the vocalization sequence (Gooler and O’Neill 1987, see fig. 1.8). There is no evidence to date that the emotional motor system in bats (anterior cingulate cortex, PAG, etc.) is organized differently than in other mammals.

Vocal utterances are themselves the result of a complex coordination of many muscles in the laryngeal, pharyngeal, and respiratory musculature (NA, ncl. hypoglossus, ncl. accessorius, spinal nerves to C1–C5, T1–T14). On the other hand, a number of coordinated motor events accompany vocalizations in parallel. The most important examples are movements of the pinnae and/or the noseleaf, middle-ear muscle contractions, and coordination with head and wing movements. The neural substrate of this coordinated control of motor behaviors has been only partially detailed. The premotor and motor nuclei for the separate efferent control circuits (facial nucleus, trigeminal nucleus, motor division) were studied in the general mammalian system and, to a lesser extent, in bats. However, the circuitry for the temporal coordination and integration of activities resulting in complex behavioral patterns is largely unknown.

Higher Level Influences on Vocal Production

Very recently the idea of separate processing pathways in the auditory forebrain has gained more support from imaging studies, as well as from neurophysiological and neuroanatomical investigations (Rauschecker et al. 1997). According to this concept, and analogous to the visual system, structural analysis of sound would be carried out predominantly in the ventral stream, whereas the spatial information on sound source location would be processed in a dorsal stream. The question arises whether and where information on the spatial location and acoustic structure are integrated for perceptions that guide behavioral responses.

There are considerable data on the cortical processing of complex sound patterns in the CF-FM bat, as well as anatomical data on the structure and connectivity of forebrain areas (see chapters 24–32 of this volume). Thus, the connection between the auditory thalamus and cortex clearly is organized in parallel pathways, distinguishing the afferent influx of the dorsal region from the ventral regions of the auditory cortex (Radtke-Schuller, chapter 30, this volume). The physiological responses clearly are different and in many respects specialized in dorsal fields of the bat cortex, in comparison to the more temporal (primary) areas.

The extralemniscal central acoustic tract contributes additional input to frontal regions of the forebrain,
Fig. 1.8. Sites in the mustached bat forebrain from which biosonar vocalizations were elicited by electrical microstimulation. The horizontal and lateral views of the brain (insets) indicate the levels of the respective sections. (a) The penetrations from which electrical stimulation elicited vocalizations are shown in this sagittal section by vertical lines located anterior and dorsal to the corpus callosum. (b) A transverse section taken from a different animal shows an HRP deposit (dark spot) midway along the rostrocaudal extent, which indicates the mediolateral position of the stimulation sites. (AC, anterior commissure; ACG, anterior cingulate cortex; CC, corpus callosum; Cd/Pt, caudate/putamen; FX, fornix; HP, hippocampus; RCC, radiations of the corpus callosum; V, lateral ventricle.) (c and d) Spectrograms (top) and associated time waveforms (bottom) of spontaneous and electrically elicited vocal pulses. The relative amplitude of harmonics is represented by the peaks of the fast Fourier transforms (FFTs) in the waterfall spectrographic display. Each FFT contains 25% new information. These signals show the characteristics common to biosonar vocalizations emitted spontaneously or elicited by microstimulation. The vocalizations typically begin with a short spectral broadening, followed by a long CF component and a terminal FM sweep. The fifth harmonic is down by 14 dB due to attenuation in the recording instrumentation. (Adapted from Gooler and O'Neill 1987.)
which have connections to the acoustic areas (Esser et al. 1997; Casseday et al. 1989). A considerable investigation should be carried out to study the details of physiological, anatomical, and connectional properties of this frontal cortical region. The idea that this cortical region represents a level of integration of the parallel auditory streams and is at the same time involved in audiomotor feedback control is compelling.

**Audiomotor Systems in the Echolocating Bat**

In this section the central neural mechanisms that support vocal control in echolocating bats are considered. The focus is on five brain regions: the central nucleus of the acoustic tract (NCAT), the superior colliculus (SC), the paralemniscal area (PLA), the rostral pole of the inferior colliculus (ICrP), and the pontine gray (PG). All regions show at least one of the following features: vocalization can be elicited by electrical or pharmacological stimulation; and the region has efferent or afferent connections with premotor structures involved in vocal control. The main characteristics of the neural response characteristics in these regions and their possible relationship to vocal control are described below.

**Activation/Deactivation Studies**

Brain structures involved in the control of motor responses or behavioral patterns can be determined by showing that their activation is necessary and/or sufficient for eliciting the behavior or that their damage or absence suppresses or disturbs relevant motor response. Among a variety of methods, electrical or pharmacological microstimulation and focal lesioning have proven to be valuable tools in this respect. However, the drawbacks of these methods (estimation of effective stimulation area, secondary effects, etc.) must be taken into account when interpreting the data. The conditions to evoke behaviors—for example, vocal responses by electrical stimulation—are not uniform in all relevant brain regions and could point to differences in the functional involvement of the specific areas.

With regard to electrically elicited vocalizations, three different patterns have been distinguished (Radtke-Schuller and Schuller 1990). In the first response pattern, the stimulation triggers sonar vocalizations at low-threshold currents (less than 20 μA) without any concurrent limb or body movements. The evoked echolocation calls are indistinguishable from spontaneously emitted calls. Stimulus and vocalizations show mostly a one-to-one relationship at a relatively constant response latency. In the second response pattern, the electrical stimulus influences the pattern of the vocalizations. Stimulation can cause distortions in the temporal or, in rare cases, in the spectral composition of the calls. In the third response pattern, vocalizations are not elicited in a one-to-one relationship to the stimulus at a distinct latency, but start after prolonged repetition of electrical stimuli. The evoked vocal responses are not synchronized to the stimulation rhythm and persist for some time even after the electrical stimulation has been switched off.

The first stimulus response pattern ("trigger type") has been encountered in five areas in the horseshoe bat's brain (Schuller and Radtke-Schuller 1990), presumably premotor parts of the descending vocal motor system. These areas are (1) the paralemniscal segmental area (PLA) located rostrally and medially to the dorsal nucleus of the lateral lemniscus (Pillat and Schuller 1998); (2) the dorsolateral parts of the mesencephalic reticular formation, corresponding to the deep mesencephalic nucleus in the rat; and (3) the intermediate and deep layers of the SC (also *Eptesicus fuscus*; see Valentine and Moss 1998), which are enormously hypertrophied in the bat relative to the visual input layers (*Eptesicus fuscus*, Covey, Hall, and Kobler 1987; *Rhinolophus rouxi*, Reimer 1989). Two further areas showing this response to electrical stimulation are the nucleus of the brachium of the inferior colliculus (NBCl) and the pretectal area (AP) at the transition between the SC and medial geniculate body (Schuller and Sripathi 1999). The shortest latencies, around 25 ms, were found in the PLA; whereas the latencies in the other regions could be longer than 100 ms.

In addition, microstimulation in these brain regions generally evokes coordinated pinna movements, another orienting behavior tightly coupled to echolocation (Menzner 1996; Schuller 1998; Valentine and Moss 1998; Valentine, Sinha, and Moss in press). In all these areas, it is sufficient to stimulate unilaterally to elicit calls. However, there is no evidence that microstimulation parameters (intensity, rate, or timing) or the locus of stimulation in the PLA or SC have a direct influence on the features of the bat's sonar vocalizations. This suggests that activity in these brain regions does not modulate the final motor pattern for echolocation sound production. These areas seem to gate vocal emissions under specific conditions. It is still unclear under which conditions the activity of these areas is necessary for the emission of echolocation calls.

Lesioning studies, however, raise questions about the importance of the PLA in Doppler-shift compensation (DSC) behavior. Bilateral lesions of the PLA of the CF-FM bat, *Rhinolophus rouxi*, do not disrupt DSC behavior (Pillat and Schuller 1998). These findings suggest that PLA is not the sensorimotor interface for echolocation in bats. Manipulation of GABAergic activity in the PLA, however, affects vocal parameters (Schuller and Sripathi 1999). These results provide evidence for modulatory influences of the PLA on vocal control. It appears that this brain region could play a role in a larger circuit for audio-vocal feedback control but is not essential to the modulation of echo-dependent vocal behavior.

In posterior parts of the pretectal area, at the transi-
tion between the SC and medial geniculate body, vocal responses are elicited at low-threshold currents with electrical stimulation. The region receives prominent afferent input from the auditory pathway—that is, the dorsal field of the auditory cortex, the inferior colliculus (central and rostral pole nucleus), and the nucleus of the central acoustic tract. Input from nonauditory structures originates in the nucleus ruber, the deep mesencephalic nucleus, and the lateral nuclei of the cerebellum. Efferent connections project back to thalamic targets (zona incerta and nel. reticularis thalami), to the nucleus ruber, the cuneiform nucleus, and distinct areas of the pontine gray. The connectivity pattern of this region suggests an important functional role of the pretectal area for acoustically guided behavior in bats. However, such function must be demonstrated by showing direct effects of manipulations of this region on vocal characteristics.

Interestingly, the PAG, an area commonly associated with vocal behavior in mammals, and the cuneiform nucleus (CUN) do not appear to be directly involved in the control of sonar vocalization parameters in the horse-shoe bat (Schuller and Radtke-Schuller 1990). The cuneiform nucleus is located lateroventrally to the PAG and medioventrally to the colliculi.

While microstimulation in the lateral parts of the PAG and in the cuneiform nucleus elicits vocalizations in the bat, the vocalizations obtained at low stimulation currents (below 20 μA) are normal echolocation calls. However, the one-to-one relationship between stimulation and calls is absent. Vocalizations also persist for some time after stimulation ceases. The vocal responses are always accompanied by arousal of the animal, which increases further with persisting stimulation.

Given its anatomical connections, the cuneiform nucleus is probably one of the relays mediating vocal control information from higher brain levels to the level of the laryngeal motoneurons. It has direct descending access to the laryngeal motor nucleus in the medulla, and it receives input from four of the five regions in which vocalizations could be elicited electrically (but not influenced in their spectral or temporal characteristics by the stimulation parameters or location within the structure). The arousal evoked by electrical stimulation of CUN suggests that this nucleus may modulate affective components of vocalizations. The fact that the structures projecting to the CUN do not directly influence spectrotemporal parameters of vocalizations upon stimulation offers further support to the notion that this nucleus might not be directly involved in vocal parameter control.

The pathway involving the cuneiform nucleus could be important for gating the production of vocalizations under distinct behavioral situations, but it does not represent a direct vocal control interface. This suggests that the PAG and CUN could be involved in activating vocal production in particular emotional states. Rather than in shaping the signals used for echolocation. In this respect, the cuneiform nucleus and adjacent periaqueductal regions in the bat compare functionally to the periaqueductal gray in primates, which is considered to be an important relay station of the descending vocalization system (Jürgens 1994).

Brainstem areas that have immediate influence on the spectral parameters of vocalization are not well defined in the bat. Loci, where electrical stimulation led to distortion of vocal parameters and thus influenced the vocal output directly, were found mostly in the vicinity of vocal areas in the lateral tegmental area and in the lateral pontine regions (Schuller and Radtke-Schuller 1990). Spectral and temporal distortion of calls can be due either to direct influence on premotor or laryngeal motor neuron pools, on descending fibers or to a temporal mismatch of respiratory and vocal control resulting from the electrical stimulation. In the latter case, the electrically initiated laryngeal response for vocalization can fall into a period of inhalation instead of exhalation, and the lack of exhalation volume can distort the calls.

The lateral pontine area yielding distorted calls and arousal is the nucleus of the central acoustic tract (NCAT), with neurons tuned to the constant-frequency component of the bat's echolocation signal. The NCAT projects to putative audiobrain control structures (see fig. 1.9) and could be a strong candidate for audio-vocal functions (Casseday et al. 1989; Behrend and Schuller, chapter 2, this volume).

In the nucleus of the brachium of the inferior colliculus (NBIC), located in a rostrolateral position to the in-

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**Fig. 1.9.** Schematic diagram of the projections from the nucleus of the acoustic tract (NCAT) to the midbrain superior colliculus (SC), suprageniculate nucleus (SG), auditory cortex, and frontal cortex. Also shown are projections from the cochlear nucleus (CN) to the superior olivary complex (SOC), nuclei of the lateral lemniscus (NLL) and to the inferior colliculus (IC), which also projects to the SC and the medial geniculate body (GMs). The schematic also shows descending projections from the frontal cortex to the auditory cortex and SC. (Adapted from Casseday et al. 1989.)
ferior colliculus, is another brain area in which vocal responses can be evoked electrically at low stimulation current. Lesioning of this structure has marked influences on Doppler-shift compensation behavior, even though the resting frequency is unimpaired (Schuller and Sripathi 1999). Connectivity and physiological response properties of this brain region are not available in the bat; and the afferent connections of this area have yet to be studied in detail.

Microstimulation in cortical brain regions also elicits sonar vocalizations without distortion of the spectro-temporal signal patterns. In the anterior cingulate cortex, the locus of microstimulation influences the features of the sonar vocalizations (Gooler and O’Neill 1987), in that the frequency of electrically elicited calls depends on the locus of cortical stimulation. In other mammals including primates, the anterior cingulate cortex is an important forebrain structure controlling vocal utterance (Jürgens and Pratt 1979; see also fig. 1.8).

Auditory Responses in Putative Prevocal Areas

Information carried by echoes guides vocal behavior of the echolocating bat. As described above, the CF-FM bat adjusts the frequency of sonar emissions to compensate for echo Doppler shifts introduced by flight velocity, achieving a relatively constant echo return at the reference frequency to which it is maximally sensitive (Schnitzler 1968).

The FM bat adjusts the repetition rate, duration, and bandwidth of sonar signals with changing target distance, using echo delay information to avoid overlap of outgoing sounds and returning echoes (Schnitzler and Kalko 1999; see also fig. 1.1).

The CF-FM bat tolerates overlap of outgoing sounds and returning echoes, because the sonar vocalizations and returning echoes stimulate separate frequency channels in the bat’s auditory system. While the Doppler-shifted echoes can differ from the sonar vocalizations by less than 0.5%, such frequency changes in the signals are perceptually distinct to the CF-FM bat, due to specializations in its auditory system (Neuweiler, Bruns, and Schuller 1980). A detailed review of auditory information processing in the bat sonar receiver is presented by Suga et al., chapter 24, this volume. Herein, the auditory input to putative prevocal areas is considered, with particular emphasis on the auditory coding of information needed to guide vocal control of echolocation signal production.

Doppler-Shift Compensation

CF-FM bats respond to Doppler shifts by adjusting sonar vocalization frequency to produce a relatively constant echo return Doppler-shift compensation (Schnitzler 1968) that isolates spectral changes in returning echoes from the wing-beat patterns of insect prey. As noted above, relative target velocity resulting in frequency changes of <0.5% is perceptually salient to some species of CF-FM bats and can trigger subsequent behavior. The neural basis for fine frequency discrimination in CF-FM bats relies on very sharp tuning in the range of a CF-FM bat’s echo reference frequency (Q10 dB values up to 400) (Neuweiler, Bruns, and Schuller 1980) and can be traced to mechanical specializations of the cochlea. Doppler-compensating CF-FM bats show in addition an expanded representation of frequencies at and a few kHz above the resting frequency throughout the auditory system (Neuweiler, Bruns, and Schuller 1980). Thus CF-FM bats are very sensitive to small Doppler shifts in sonar echoes, which in turn support Doppler-shift compensation behavior in which the bat adjusts sonar vocalizations to stabilize returning echo frequency (see fig. 1.2).

The Doppler-shift compensation system in the horsehoe bat and in the mustached bat is a model example of an automotor feedback system and lends itself to investigating the mechanisms and underlying structural organization of information transfer from the auditory system to the vocal control system. There is evidence that neurons in the paralemniscal tegmental area (PLA) of the Doppler-shift compensating horseshoe bat (R. rouxi) are involved in audio-vocal interactions. Metzner (1989, 1993, 1996) found a population of audio-vocal neurons whose responses were influenced by sonar signal production (see fig. 1.10). He located neurons in the rostral region of the PLA that were active before and/or during vocalizations with little or no response to auditory stimuli (vocal neurons). Neurons in more caudal regions were active during or after sonar vocalizations and also to acoustic stimuli (auditory or audio-vocal neurons). Most audio-vocal neurons had best frequencies in the band relevant for DSC and exhibited a large activity change within a small frequency increase (see below, auditory responses in “nonprimary” auditory areas). The concurrent occurrence of vocal, audio-vocal, and auditory neurons in this restricted area suggests a putative role of the PLA in the interaction of auditory and vocal systems. Suga and Yajima (1988) also described audio-vocal responses in the midbrain of the mustached bat.

The nucleus of the central acoustic tract (NCAT) in the horseshoe bat, R. rouxi, consists largely of neurons with best frequencies at and in a narrow frequency band above the bat’s resting frequency with very narrow tuning (Schuller, Covey, and Casseday 1991). More than 60% of the neural population is devoted to processing sound frequencies in the region of the constant-frequency (CF) portion of the bat’s echolocation call. Such overrepresentation of the CF frequencies hints to an involvement of the region in the analysis of spectral fine structure of the echo. On the other hand, these neu-
vestigation is needed to develop a complete understanding of the functional role of the NCAT in audiomotor control.

Spatially Guided Behaviors

Central to the control of sonar signal production in the FM bat is target distance information. As described above, the echolocating bat estimates target range from the time delay between sonar emissions and returning echoes. Psychophysical experiments suggest that CF-FM and FM bats both use the FM component of the sonar signal for target distance measurement (Simmons 1973). The neural basis for target ranging has been studied extensively, and researchers hypothesize that echo-delay-tuned neurons play a central role in distance measurement by echolocating bats. Echo-delay-tuned neurons, found in the auditory brainstem (Mittman and Wenzel 1995; Dear and Suga 1995; Valentine and Moss 1997), thalamus (Olson and Musil 1992), and cortex (O’Neill and Suga 1982; Wong and Shannon 1988; Dear et al. 1993), show very weak responses to single FM sounds. However, these neurons respond vigorously to pairs of FM sounds (a simulated pulse and a weaker echo) separated by a delay. Typically, echo-delay-tuned neurons show facilitated responses to simulated pulse-echo pairs over a delay range of several milliseconds. The delay to which an echo-delay-tuned neuron shows the largest response is referred to as the best delay (BD). In CF-FM bats, BD is organized topographically in the auditory cortex (O’Neill and Suga 1982); but in FM bats, there is no evidence for an orderly representation of BD (Dear et al. 1993; Wong and Shannon 1988). (The neural basis for target ranging in echolocating bats is described in detail in part 2 of this volume.)

In the SC of the FM bat, Eptesicus fuscus, about 33% of the auditory neurons sampled showed echo-delay tuning, a response characteristic that could be used by the bat to guide vocal behavior. Best delays for the population of echo-delay-sensitive SC units were largely between 8 and 16 ms, corresponding roughly to 1.4–2.7 m target distance. Responses of echo-delay-tuned neurons showed selectivity to echo arrival time that was often tagged to the azimuth of stimulation. A majority of echo-delay-tuned neurons exhibited facilitation along the delay axis only from a restricted azimuth within the cell’s two-dimensional receptive field (Valentine and Moss 1997).

In the horseshoe bat, relatively few neurons in the SC showed responses to vocalizations, which in most cases resembled responses to acoustic stimuli mimicking vocalizations (Reimer 1991). About one third of the neurons active during vocalization could not be driven by comparable acoustic stimuli. Vocally active neurons in the SC did not discharge prior to the emission of the calls but always with a latency of some milliseconds af-
ter the start of the vocalization. Latency to vocalization often was shorter than to passive acoustic stimulation. The auditory response to pure tones in the intermediate and deep layer SC neurons was primarily tuned to frequencies at and above the resting frequency of the bat, whereas the remaining sound frequencies were underrepresented. The frequency tuning was relatively narrow with Q10 dB values often above 80, in contrast to broad frequency-tuning measurements in cats. In CF bats narrowband noise was less effective as a stimulus than pure tones.

More than two thirds of the SC neurons in the horseshoe bat showed a binaural response, which was in most cases characterized by contralateral excitation and ipsilateral inhibition of the response. The inhibition was effective for ipsilateral interaural intensity differences greater than 10 dB on the ipsilateral side, so that signals from frontal directions were processed best. This finding is consistent with the importance of target reflections from straight ahead for echolocation. The SC showed a topographical trend for interaural intensity differences with representation of more ipsilateral positions in medial portions and more contralateral positions in lateral parts of the nucleus. The SC seems to be more involved in functional mechanisms for directional encoding and control of orientation in space (e.g., pinna orientation) than in audio-vocal feedback control. The SC could participate in the temporal coordination of vocal utterances and pinna and orientation movements (Valentine and Moss 1998). The rostral pole nucleus of the inferior colliculus (ICrP) is important for audiometer interaction on the basis of anatomical connections with various nuclei of the ascending auditory system and premotor structures. The auditory responses of ICrP neurons are grouped into roughly two areas: a medial tonotopically organized region and a lateral nontonotopic region with many complex response patterns and strong inhibitory influences. Throughout the ICrP an overrepresentation of the frequencies of the final frequency-modulated part of the bat’s echolocation call can be found (Precht 1995). This predominance of neural processing in the FM frequency range suggests that audiometer functions of the ICrP are related to acoustically guided behavior in which the final FM portion is of major importance. Thus, the ICrP could mediate in the temporal coordination of vocalizations and pinna movements, but it is most probably not important for Doppler-shift compensation. Somatosensory projections to the ICrP and the external nucleus of the IC hint to the integrative functions of these marginal IC subnuclei for multisensory information processing.

The pretectal area receives very dense auditory projections from almost all levels of the auditory pathway (NCAT, IC, dorsal field of the dorsal auditory cortex) and exhibits projections to premotor areas. Therefore, it could be an important structure for audiometer behavior. However, information on auditory responses of pretectal neurons is not available to date.

Conclusions

The echolocating bat uses dynamic acoustic information about the position and velocity of a target to make rapid and fine adjustments in the features of sonar vocalizations. Echo-dependent adjustments of the frequency, duration, and timing of echolocation calls require a sensorimotor interface, where acoustic information carried by sonar echoes is used to guide motor commands for vocal production and control. Investigations into the neural mechanisms of audio-vocal interaction have demonstrated that several nuclei on different brain levels show anatomical connections and functional response characteristics that would suggest their role in audio-vocal feedback for echolocation in bats. Certainly, the view that distinct structures mediating the transformation of Doppler-frequency shifts into a motor signal for lowering the emitted call frequency, as in the seemingly simple Doppler-shift compensation system, must be modified. Instead, we propose an interwoven network of audio-vocal control on many different brain levels. Further research to clarify the contribution of each potential interfacing brain structure and the neuroanatomical details of the circuitry is needed to come closer to an understanding of audio-vocal control mechanisms in echolocating bats. Comprehension of audio-vocal mechanisms in such a sophisticated hearing-oriented system like echolocation will advance our knowledge of audio-vocal interactions in less specialized mammals.

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