

Sensorimotor Integration in Bat Sonar

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As an echolocating bat pursues its insect prey, it actively probes the environment with ultrasonic signals and listens to the echoes that return from reflecting targets (Griffin 1958). Information carried by the echoes is processed by the bat's sonar receiver to determine the direction and distance of insect prey, and this spatial information is then used to guide adjustments in the position of the head and pinnae, in the activity of the muscle groups controlling the flight path, and in the production of subsequent sonar signals (Busnel and Fish 1980; Nachtigall and Moore 1986; Fay and Popper 1995). The bat's biosonar system thus requires a sensorimotor interface in which spatial information computed by the central nervous system directs motor commands for appropriate orientation behaviors. The emphasis of this chapter is on the neural mechanisms that support this sensorimotor feedback system in the echolocating bat *Eptesicus fuscus*.

Anatomical and neurophysiological data suggest that many interconnecting neural structures support sensorimotor integration in bat sonar; these include the midbrain superior colliculus, cerebellum, and pontine reticular formation, as well as other brain regions (Huffman and Henson 1990; Covey and Cassedy 1995). Our particular focus

has been on the superior colliculus (SC) of the bat, and we here present data from behavior-lesion studies, extracellular recording, and microstimulation experiments that suggest biologically relevant specializations in the SC of the bat used for acoustic orientation by sonar. We also present a model that describes the bat SC as part of a complex interactive system which coordinates vocalizations and orientation maneuvers to the reception of echoes.

The bat's auditory system receives echoes and other sounds in its environment and processes this information for spatial perception using acoustic cues. However, the bat essentially has a "standard mammalian auditory system" (Suga 1988; Covey and Cassedy 1995). Many of the same cues used by other mammalian species to localize sound and to process complex patterns of acoustic information are exploited by the bat for orientation and perception by sonar. Binaural cues for sound localization are used by the bat to estimate the azimuthal position of an acoustic target. Monaural cues are important to bats for assigning a location in azimuth, but these also are considered essential for determining the elevation of a sound in space (Heffner and Heffner 1992).

The bat's two pinnae and tragi produce changes in the

spectrum of incoming echoes, creating patterns of interference that it uses to estimate target elevation (Grinnell and Grinnell 1965; Lawrence and Simmons 1982; Mogdans et al. 1988; Wotton et al. 1995). Interaural spectral cues produced by the directionality of the two ears may provide additional information for determining target angle in the vertical plane (Grinnell and Grinnell 1965). The third spatial dimension, target range, is conveyed by temporal cues produced by echo reflections of the bat's sonar emissions. The delay between an outgoing vocalization and a returning echo corresponds to the distance between the bat and its target (Hartridge 1945; Simmons 1973). During target pursuit, the bat tailors its vocalizations and regulates its hearing as distance and echo amplitude change (Cahlander et al. 1964; Hartley 1992).

The bat also maneuvers its flight, aims its head, and focuses its ears as it pursues its target. Changes in the position of the bat's head and pinnae may enhance the information carried by these binaural and monaural cues for sound localization, just as a person gazes at an object to gain more detailed visual information. The directionality and motility of the bat's auditory receiver, relative to the external auditory field, allow the animal to actively sharpen its perception. The characteristics and temporal patterning of its echolocation sounds constrain the acoustic information available to the bat's sonar receiver.

A neural mechanism for orienting by sonar toward an acoustic target would likely involve a three-dimensional representation of auditory space that includes information about the current and desired position of the head and ears and about the timing and features of each vocal emission. Converging lines of evidence from comparative anatomical, physiological, and behavioral studies suggest that the midbrain SC links auditory spatial perception with motor pathways for acoustic orientation (Jen et al. 1984; Poussin and Schlegel 1984; Wong 1984; Covey et al. 1987; Cassedy et al. 1989). The mammalian SC contains multimodal sensory inputs that are topographically organized in spatial registration, and motor circuitry which controls orientation behavior (Stein and Meredith 1993). We hypothesized that this midbrain structure may reveal distinct functional specializations in the bat that are important for its acoustic orientation.

The SC has connections with many structures in the auditory brainstem and midbrain, receiving multiple inputs at different stages of processing. It receives inputs from cortical areas that may be involved in processing target-range information and in controlling vocal behavior (Cassedy et al. 1989). The SC also receives input from the accessory or extralemiscal central acoustic tract. A fast route to thalamocortical structures, the central acoustic tract by-

passes the central nucleus of the inferior colliculus (ICC) (Papez 1929; Cassedy et al. 1989), and thus forms an ascending auditory pathway in parallel with the main auditory tract. Moreover, the extensive connections of the SC with pontine and reticular structures, and with the periaqueductal gray, trigeminal, and olivocerebellar systems, support its role in acoustic orientation, acoustic reflex production, and audiovocal control. In both the SC and the descending acousticomotor system, microstimulation reliably elicits vocal behavior in echolocating bats (Schuller and Radtke-Schuller 1988, 1990; Metzner 1993; see following). We have investigated the role of the SC in a sensorimotor feedback system that coordinates the bat's active motor control over the acoustic features of reflected echoes. Because the directional control of echolocation behavior is closely linked to changes in target position (Kick and Simmons 1984), a system of sensorimotor feedback in the SC must include spatioacoustic information in azimuth, elevation, and range.

Sensorimotor Feedback in Bat Echolocation Behavior

Field and laboratory observations have documented adaptive behaviors exhibited by echolocating bats in the pursuit of insect prey (Griffin 1958; Griffin et al. 1960; Webster 1963a, 1963b; Webster and Brazier 1965). High-speed motion pictures show that a bat approaching an insect locks its head onto the target, even when the bat is unable to maneuver its body to the target's exact position (Webster 1963a, 1963b). As a bat flies toward a target, changes in the repetition rate, bandwidth, and duration of its sonar emissions have been used to divide the bat's insect pursuit sequence into different phases: search, approach, and terminal (Griffin et al. 1960; Webster 1963a, 1993b; Schnitzler and Kalko, Chapter 12, this volume).

Laboratory Studies of Insect-Capture Behavior

We conducted studies of bats capturing insects in a large laboratory flight room to detail adaptive motor behaviors in an acoustic orienting task and to provide a behavioral assay to anchor our neurophysiological studies of sensorimotor integration in bats. In these studies, insects were tethered to a string attached to a rotating turntable mounted on the ceiling of a large flight room, and blinded bats were trained to intercept these moving insects on the wing while their behaviors were recorded on high-speed video (Eastman Kodak, 500 frames/sec) and audio tape (Racal Store 4, 30 inches/sec).

The bat's success rate and motor behaviors required for the task were measured during a 3- to 4-week period

to document baseline performance. Our video analyses showed that the bat typically positioned its head 3–4 cm above the tethered insect at the point of capture, locking the position of its head with an accuracy of approximately 5°. The bat then scooped the insect into its tail membrane, transferred the prey item to its mouth, and continued in flight. Sonar sounds recorded from the animal showed a systematic increase in repetition rate, decrease in duration, and change in overall bandwidth with decreasing target distance (Figure 15.1). This pattern of sound production resembles that recorded from *Eptesicus fuscus* foraging in the field (Griffin 1958).

Our analysis of sounds produced by the bat in this capture task revealed that the sound repetition rate of *E. fuscus* during target pursuit does not change continuously over time but rather remains stable for fixed intervals before increasing. During the approach phase, the sound repeti-

tion rate may plateau at about 30 Hz for time periods as long as 150 msec (Iannucci 1993; Moss et al. 1996) (see Figure 15.1). A review of the literature uncovered this pattern of vocal production in data collected more than 40 years ago from *E. fuscus*; however, this pattern of stable repetition rates was never explicitly described (see Griffin 1953, Plate 2). In other species of bats, the pattern of vocal production is tied to respiration and wingbeat cycles (Schnitzler and Henson 1980), and this also appears to occur in *E. fuscus* (see Figure 15.1C). Note that the sound amplitude is modulated in the terminal phase of insect pursuit without the discrete breaks in sound production that appear in the approach phase.

The stable periods of sound repetition rate produced by *E. fuscus* in the approach phase of insect pursuit may provide insight into the bat's ability to process sequences of spatioacoustic information. For example, the duration of

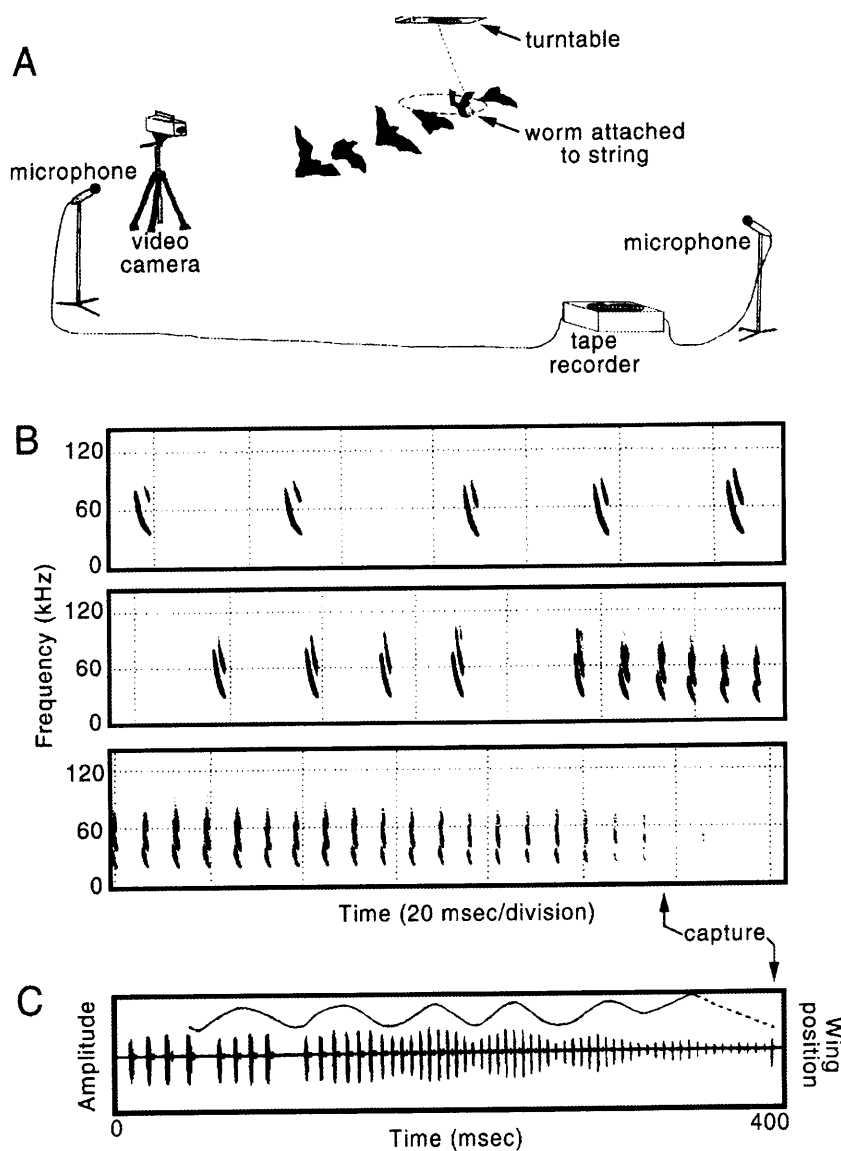


Figure 15.1. Observation of a bat's motor behaviors in an acoustic-orienting task (insect capture). (A) Setup for laboratory observation (video and sound recording) of a bat engaged in an insect-capture task. (B) Spectrograms of sound sequence produced by a bat during insect-capture task. The three panels represent a continuous sequence. (C) Time waveforms of sounds produced by a bat during the final 400 msec of an insect-capture sequence and the corresponding wingbeat cycle during this period.

these stable periods and the number of echolocation sounds contained in each may reveal behavioral response latencies for processing of distance information because the bat adjusts its repetition rate appropriately for particular echo delays (Cahlander et al. 1964).

Insect-Capture Behavior Following Lesions in the Superior Colliculus

We conducted behavioral studies to evaluate the role of the midbrain SC in an insect-capture task in the laboratory. After establishing baseline performance in the task based on an approximately 85% successful capture rate, we electrolytically lesioned the SC in two animals. The bat's post-lesion performance was carefully studied for 6–8 weeks, using high-speed video and sound recordings to document the bat's behavior (Sheen et al. 1995; Valentine et al. 1995). We found that insect capture was disrupted by the lesions, and the magnitude of the bat's deficit appeared to be related to the size of the lesions, which were confirmed histologically and confined to the SC. During a period of 4–6 weeks, recovery of performance was observed (Figure 15.2). Obstacle avoidance and landing behavior were not affected by the lesions. Sonar sounds also appeared unimpaired by the lesions and resembled those of an unlesioned bat (such as in Figure 15.1B).

Wenstrup and Suthers (1981) studied wire-avoidance behavior in *E. fuscus* that were subjected to lesions of the SC and reported similar observations. Sonar vocalizations were unimpaired, and flight behavior could not be distinguished from prelesion measurements. Three animals with

large lesions that included the periaqueductal gray (PAG) exhibited a small but statistically reliable decrease in wire-avoidance performance. Five other experimental animals with lesions restricted to the caudal SC showed no change in postlesion performance. Our work indicates that lesions restricted to the SC disrupt goal-directed behaviors such as insect capture in the bat, a finding consistent with the idea that the SC supports species-specific orienting behaviors, such as echolocation.

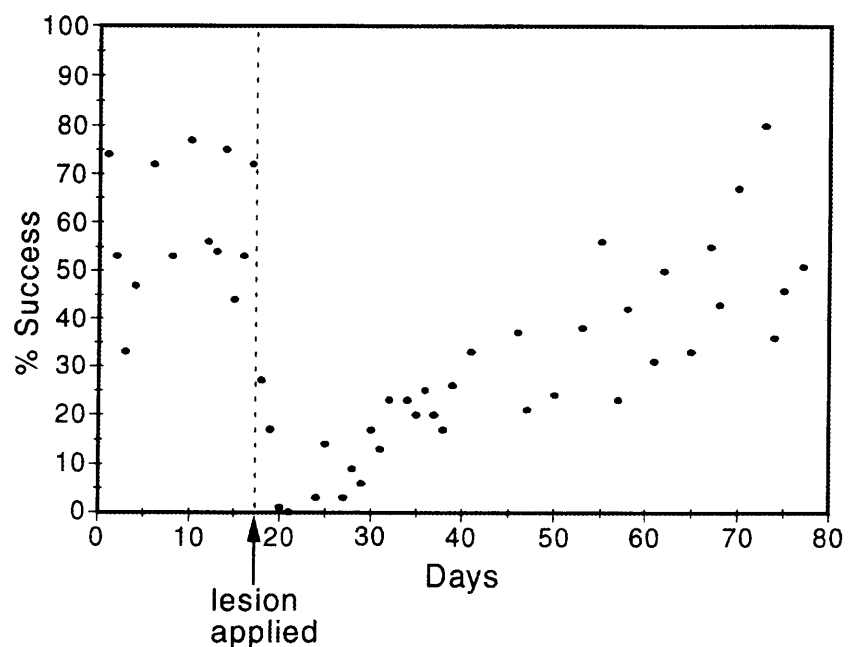
Neurophysiological Studies of the Bat Superior Colliculus

The effect of SC lesions on the sensorimotor behavior required for insect capture in *E. fuscus* suggests that there may be specialization in this neural structure for acoustic orientation by sonar. To explore this hypothesis, we conducted studies of the neural response characteristics and motor organization of the bat SC.

Extracellular Recording

Using extracellular recording methods and auditory stimulation under free-field conditions, we studied the responses of SC neurons in *E. fuscus* for evidence of spatial selectivity in three dimensions (Valentine and Moss 1993, 1997). Ninety-eight isolated units were studied in the awake animal using computer-generated frequency-modulated (FM) sounds characteristic of those produced by *E. fuscus* during the approach phase of insect pursuit (Webster and Brazier 1965). Azimuthal sensitivity was studied by recording re-

Figure 15.2. Behavioral performance of a single bat in an insect-capture task. Baseline data (i.e., from before the lesioning of the superior colliculus) are to the left of the vertical dashed line.



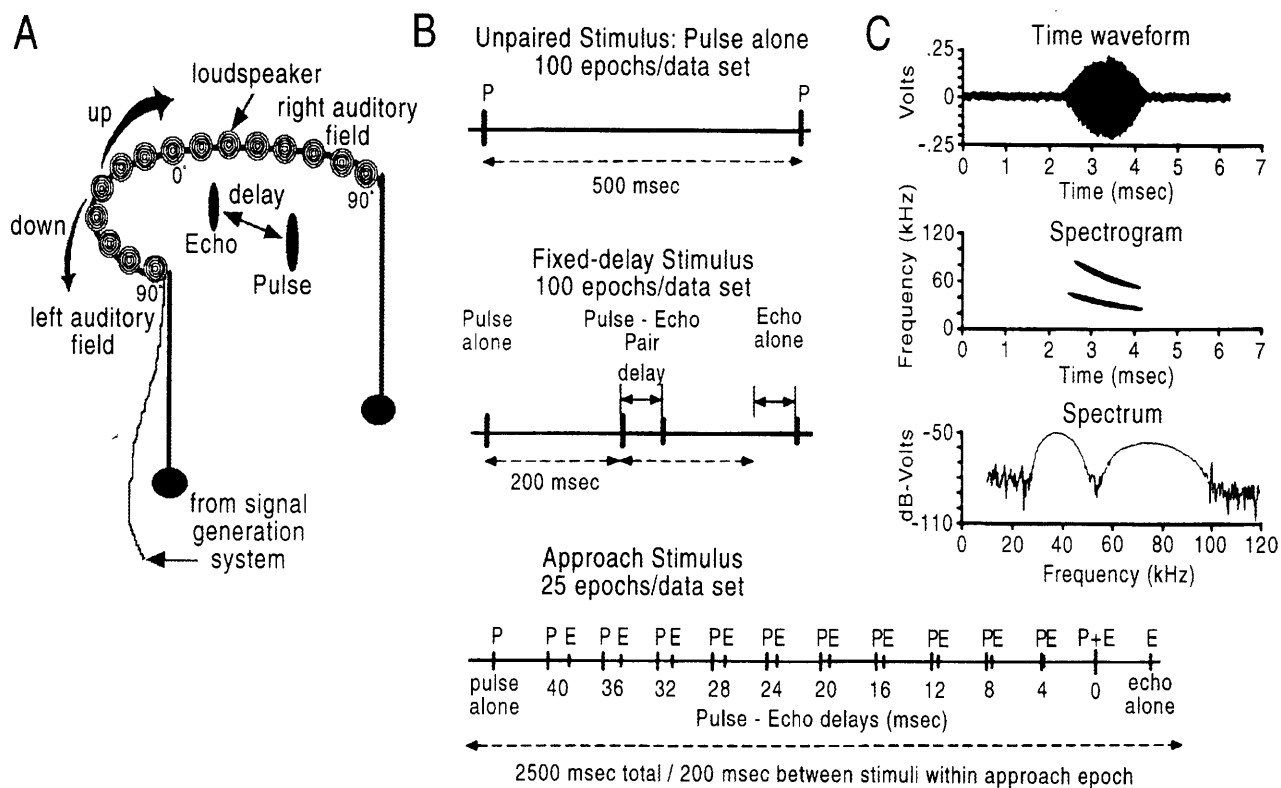


Figure 15.3. Experimental setup for determining spatial selectivity (in terms of azimuth and elevation) of neurons of the bat superior colliculus (SC). (A) Equipment for manipulating the direction and distance of acoustic stimulation. (B) Stimulus epochs (unpaired sound, fixed delay, and approach sequence) of stimuli broadcast through loudspeakers. The pulse and echo were 2-msec frequency-modulated sounds, with the echo 20 dB weaker than the pulse. (C) Sound characteristics (time waveform, spectrogram, and spectrum) of the broadcast stimuli.

sponses to acoustic stimuli broadcast through each of 15 loudspeakers arranged in a frontal hemifield around the bat (Figure 15.3A). The speaker hoop was rotated to move the sound source along the vertical axis to test sensitivity to changes in elevation. Target range was simulated using pairs of computer-generated FM bat sounds separated by particular delays (Suga and O'Neill 1979). The pulse (P), intended to mimic the bat's own sonar emission, and the echo (E), intended to mimic a target reflection, were synthesized in two separate channels and could be modified independently. The echo was attenuated 20 dB relative to the pulse.

Two neuronal populations were distinguished by their selectivity to synthetic echoes and to the spatial location of auditory stimulation. Two-thirds of the population (66/98) responded to auditory stimuli arriving predominantly from a central region of space. These cells did not show facilitation to synthetic P-E pairs in which the delay between the sounds in the pair corresponded to target range; rather, their spatial response area was defined as two dimensional (2-D). A second class of cells (33%; 32/98) were distinguished by a facilitated response to the paired acoustic stimulus (Figure 15.4A) that was coupled to spatial selectivity in azimuth and elevation (Figure 15.4B). That is, echo sensitivity in this

population depended on both the time interval separating P and E signals and the location of the sounds, indicating these cells may encode the spatial locus of an acoustic object in three-dimensional (3-D) coordinates.

The range of best delays recorded from the population of 3-D neurons was 4–20 msec (mean, 13.5 ± 8.1 msec), corresponding to a target distance of about 0.68–3.40 m. On average the number of spikes fired per stimulus presentation to the paired stimulus at the P-E delay value eliciting the maximum discharge was 7.2 times greater than the response to a single-sound stimulus at any sound level. These facilitated responses cannot be explained by the summation of stimulus energy from the paired P-E stimuli, as the auditory integration time of the bat *E. fuscus* is only about 2 msec (Surlykke and Bojesen 1996). Presenting a sequence of P-E stimuli such that the time interval between the paired sounds progressively decreased from longer to shorter delays (closing distance) or reversing the order to present short-delay pairs before long-delay pairs (increasing distance) evoked the same delay-selective responses.

Responses of 3-D neurons showed selectivity to echo delay that was tagged to the azimuth (and elevation) of stimulation (Figure 15.4B). In 68% of these cells (19/28), facilitation was exhibited along the delay axis only from a

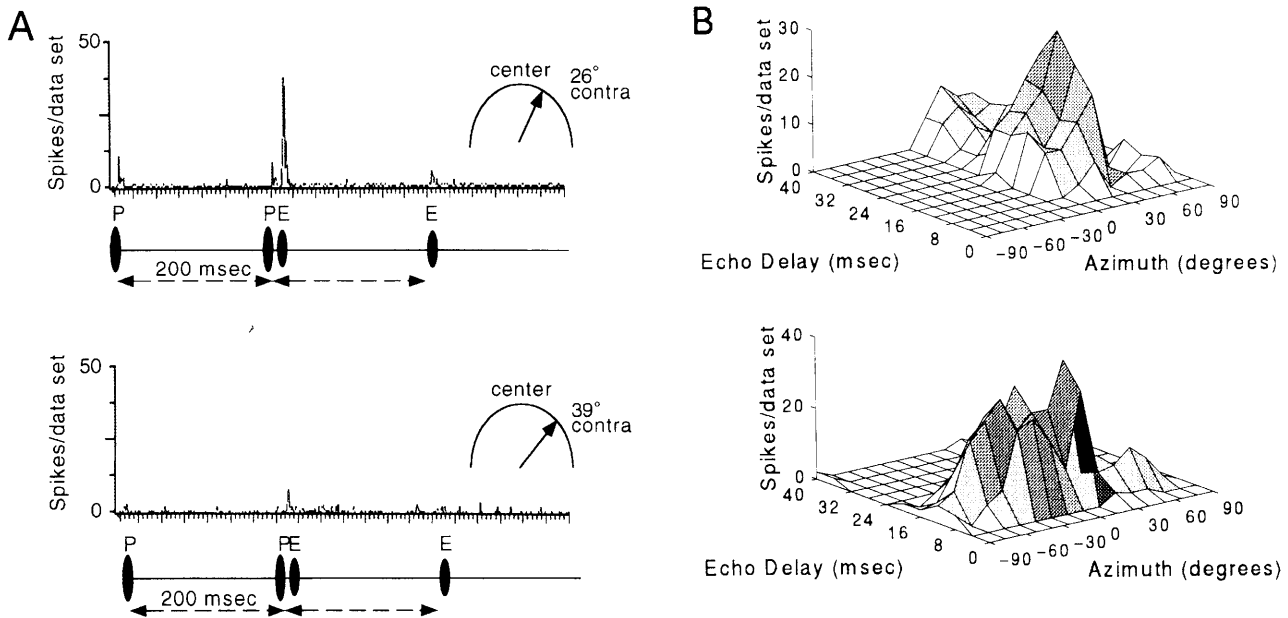


Figure 15.4. Spatial selectivity of bat SC neurons. (A) Response of a single neuron stimulated with a pulse alone (P), a pulse-echo pair with a 12-msec delay (P-E), and echo alone (E) broadcast through a loudspeaker positioned 26° and 39° off the bat's midline and contralateral to the recording site. These plots illustrate that echo-delay facilitation depends upon the azimuth of stimulation. (B) Three-dimensional response profiles of two different neurons to stimuli varying in azimuth and pulse-echo delay. The top plot illustrates the spatial response profile of a neuron with relatively narrow azimuthal tuning and relatively broad echo-delay tuning; the bottom plot illustrates the spatial response profile of a neuron with relatively broad azimuthal tuning and relatively narrow echo-delay tuning.

restricted azimuth, whereas in 21% (6/28), selective delay tuning was observed across a broad region of auditory space. No map of best echo delay was identified in the SC. This finding is consistent with neurophysiological observations on the auditory cortex of this species, which also appears to lack a topography of echo delay (Dear et al. 1993a, 1993b). The organization of best azimuth in 2-D and 3-D cells also did not reveal an orderly topography, a result that supports earlier work in the bat SC (Jen et al. 1984; Poussin and Schegel 1984; Wong 1984). Further, we found that the 2-D and 3-D populations were not segregated although 3-D cells tended to be found in the anterior and midregions of the SC.

Microstimulation

Acoustic information about target location might be expected to coordinate appropriate orienting responses in the bat, for example, head and pinna movements, as well as sonar vocalizations. To study the motor organization of the bat SC, we conducted microstimulation experiments in 14 adult animals, and responses were studied under both head-fixed and head-free conditions (Valentine et al. 1994; Valentine 1995). Single trains of constant-current, electrically isolated twin pulses were generated at a pulse rate of 100–200 Hz by a Grass S48 stimulator and stimulus isolation unit (model PSIU6). The twin-pulse stimulus proved

sufficient to activate premotor circuitry for producing orienting responses. Motor and vocal responses were simultaneously recorded on video (Canon, 30 frames/sec; Redlake, 300 frames/sec) and audio tape (Racal Store-4).

Microstimulation of the bat SC elicited pinna, head, and body movements similar to those reported in other species (Stein and Clamman 1981), revealing a motor map of the bat SC similar to that which has been observed in other mammals (Figure 15.5A,B). Microstimulation also elicited sonar vocalizations, a motor behavior specific to the bat's acoustic orientation by sonar (Figure 15.6A,B; see also Schuller and Radtke-Schuller 1988, 1990). When microstimulation was carried out in the same animal under head-fixed and head-free conditions using the same stimulation parameters, 50% (5/10) of the stimulation sites that elicited vocal-motor responses did so only when the bat's head was free to move. This result suggests a coupling may exist between the occurrence of a head movement and the output of the bat's orienting vocalization system.

The properties of the pinna movements under both head-fixed and head-free conditions were consistent with the placement of the electrode at the same site under the head-fixed and head-free testing conditions. The placement of the electrode in the tissue was confirmed histologically: The site was approximately $500\ \mu\text{m}$ from the periaqueductal gray, a midbrain region known to play a role in vocalization (Jürgens and Pratt 1979). Thus our results provide

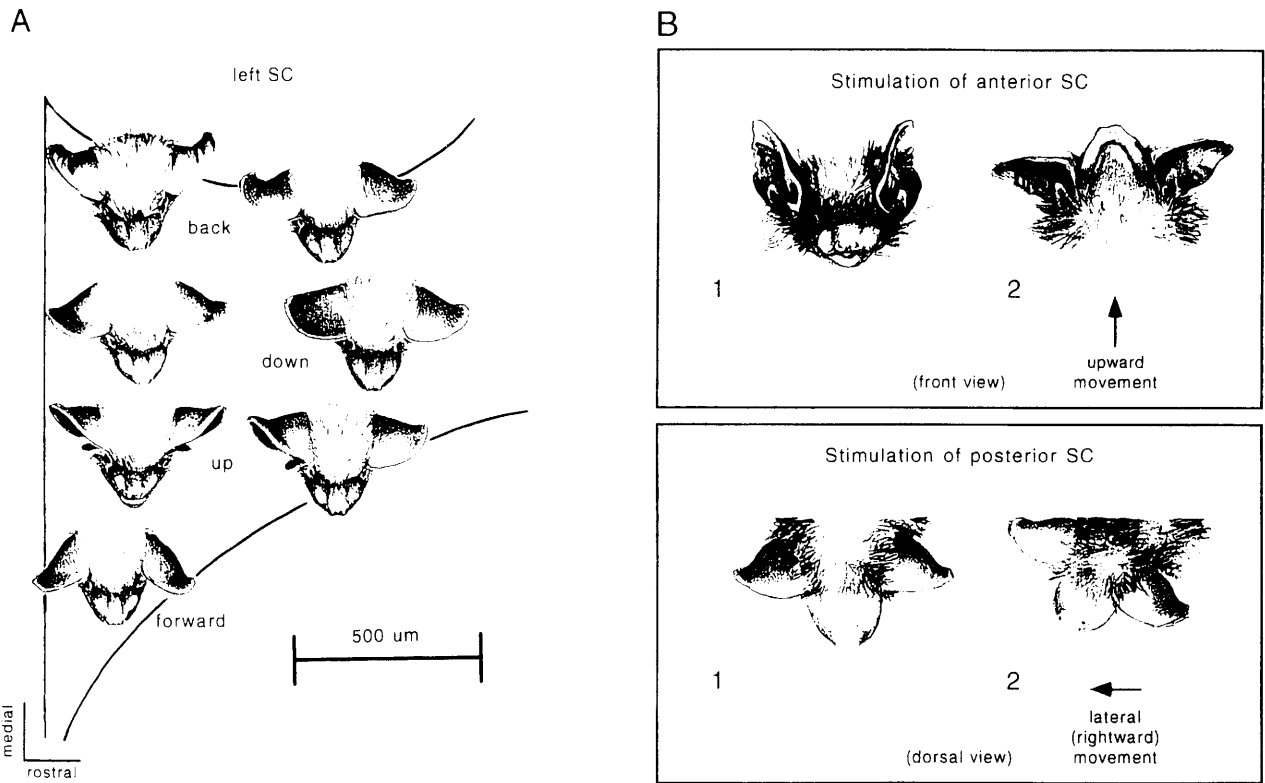


Figure 15.5. Movements elicited by microstimulation of the SC of a bat. (A) Map of pinna movements on dorsal surface of the SC. (B) Head movements with respect to initial position: upward when stimulus is applied to the anterior SC, and lateral when it is applied to the posterior SC.

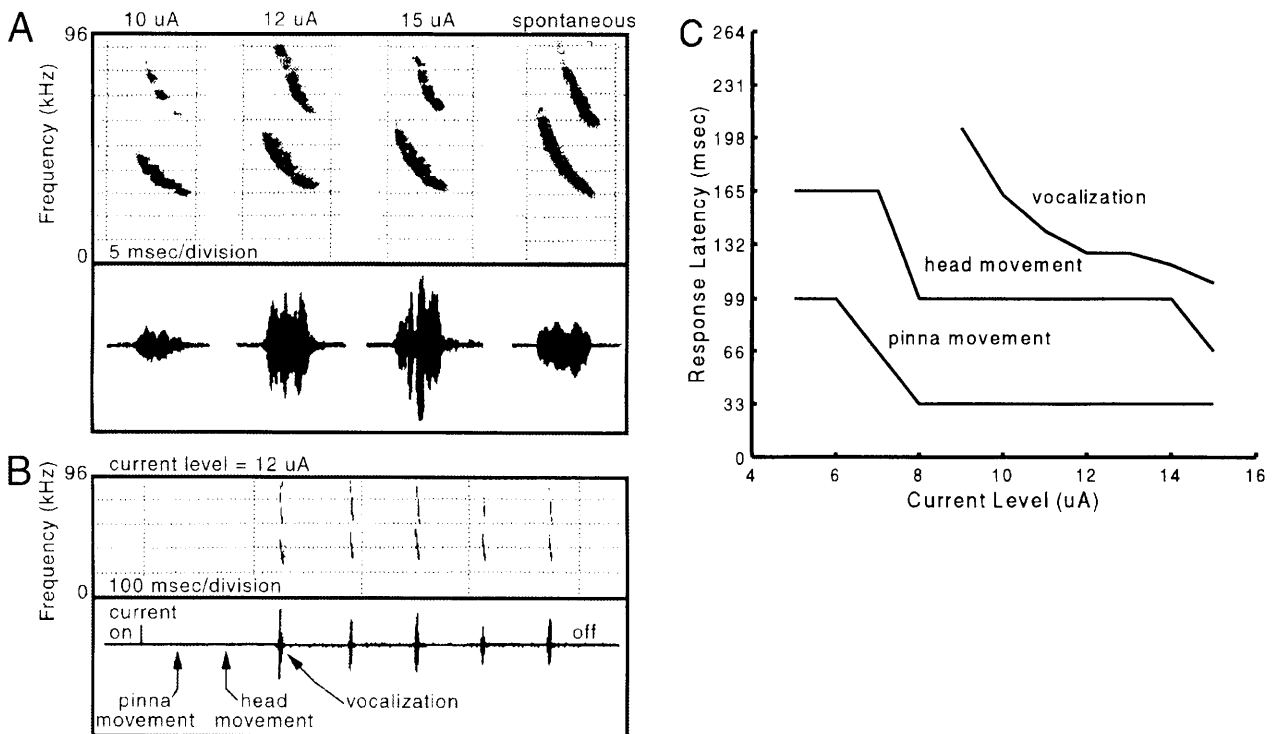


Figure 15.6. Role of the SC in motor and vocal orienting responses. (A) Sonar vocalizations elicited by microstimulation of the bat SC at different levels of current. Spontaneous vocalization recorded from a bat outside of the microstimulation experiment is also shown. (B) Temporal relation between pinna movements, head movements, and sonar vocalizations elicited by SC microstimulation. (C) Latency to initiation of vocalization, pinna movement, and head movement as a function of current strength.

convincing evidence for the role of the SC in vocal-motor orienting responses.

The current threshold for producing a detectable response was determined using a single train of twin pulses that were presented at a rate of 100 Hz. The stimulus pulse duration was 0.3 msec. The criterion for determining stimulus threshold in this study was a twitch of the pinna or neck muscle detectable on the video image. Vocalization threshold was defined a single vocal pulse emitted in response to a single train of the stimulating current. *Eptesicus fuscus* did not spontaneously vocalize during the testing, and vocalizations were observed only as a consequence of stimulation. Stimulus threshold was lowest for pinna movements and highest for vocalizations, although the difference in the amount of stimulation required to produce a vocalization was small.

The relationship between current strength and the time to initiate a behavioral response decreased as the current strength increased above the minimum threshold and showed saturation at suprathreshold current levels. In agreement with DuLac and Knudsen (1990), who studied orienting gaze behavior mediated by the tectum (SC) in the barn owl, we found that the direction of the evoked movement depended on the site of stimulation, while the metrics of the motor response (e.g., amplitude and latency) were determined by both the site and the magnitude of the stimulating current. Response latencies for eliciting head or pinna movements and sonar vocalizations in the same trial are shown in Figure 15.6C. Each curve in this plot follows a similar relationship to increasing levels of electrical stimulation. In this example, a fine measurement of response latency for the movements was not available, but by counting the number of frames from the onset of the stimulating current to the first twitch of the neck or ear flap, the latency could be determined within 33.3 msec (1 frame). In experiments carried out for two bats, a high-speed digital video system was used (Redlake, 300 frames/sec). The results of these experiments suggest the shortest latency to a twitch of the contralateral ear was of the order of 16–21 msec. This plot also emphasizes the order in which motor responses were executed. Pinna movements typically were initiated first, followed by a movement of the head. Vocalizations occurred with the longest latency, lagging behind the head movement by tens of milliseconds.

A Model of Superior Colliculus Function in the Echolocating Bat

The bat orients toward targets using mechanisms common to other species: Two-dimensional spatioacoustic cues processed by SC neurons sensitive to target locations in azi-

muth and elevation may function to direct the aim of the head and pinnae to a desired position. As diagrammed in Figure 15.7A, a signal of motor error derived from the current position of the head and pinnae and from information about the 2-D location of a target (desired position of the head and pinnae) is processed by SC circuitry and relayed to premotor and motor centers that encode the appropriate commands to the muscles. A "moving hill" of neuronal activity across the SC is thought to form the mechanism by which a population response is translated into discrete and specific movements of the head and pinnae (Munoz et al. 1991; Guitton 1992).

Although 2-D cells may coordinate orientation responses appropriate for the bat's position in 2-D space, the population of 3-D cells may direct echolocation behavior that is also coupled to target range. We suggest that the activity of 2-D and 3-D cells determines a pattern of integrated sensory information tagged with spatial coordinates in azimuth, elevation, and range, shown in Figure 15.7B as a facilitated population response. As echoes return from different distances, the temporal and spatial pattern of neural discharges in the SC may encode echo-derived spatial information as a signal of dynamic motor error for the control of acoustic orientation by sonar. The signal of a dynamic relationship between the current position of the bat with an estimate of its desired position relative to the source of salient echoes would guide appropriate head and pinna movements and vocalizations appropriate for tracking the target.

Our single-unit data, combined with microstimulation experiments, suggest that the bat SC may play an important role in the approach phase of insect pursuit (Table 15.1). Specifically, the features of the sonar vocalizations elicited by microstimulation resemble those produced by the bat during target approach. In addition, the best delays of 3-D neurons correspond to the operating range of this behavioral phase of insect capture.

Conclusions

The results of our experiments suggest that the sensorimotor function of the bat SC follows a general mammalian plan while it also supports specializations that may be important for acoustic orientation by sonar. The sensorimotor specializations we have found in our studies may play an important role in coordinating acoustic information about the position of a target with premotor and motor circuitry that permits a bat to adjust the position of its head and pinna and the features of its sonar vocalizations in response to spatial information contained in sonar echoes. It has been our goal in these studies to apply the findings from a specialized animal system to broaden our understanding of

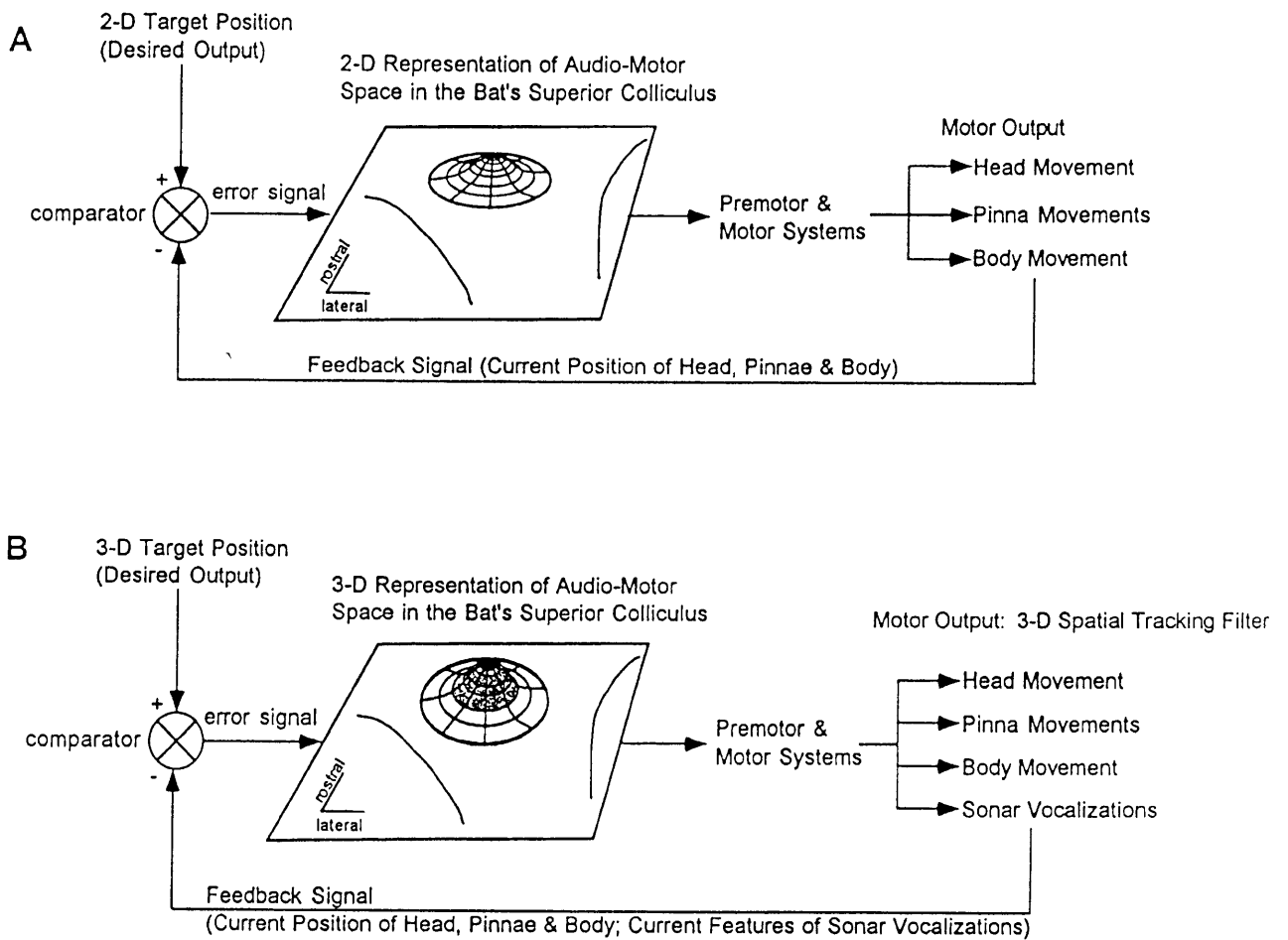


Figure 15.7. Model diagramming the role of the bat SC in the translation of spatioacoustic information into signals that produce adaptive changes in echolocation behavior: (A) translation of two-dimensional information; (B) translation of three-dimensional information.

Table 15.1

Role of the Bat Superior Colliculus (SC) in the Approach Phase of Insect Pursuit

Aspect of echolocation	SC function and properties ^a	Behavior of echolocating bat ^b
Operating range	For 3-D neurons of SC: 2.30 ± 1.38 m (0.68–3.40 m), with delay of 13.5 ± 8.1 msec (4–20 msec)	Bat is 0.5–3 m from the insect it is pursuing
Resolution of image	Coarse delay (range) tuning	After detection, the bat may pursue a moving target without fine image resolution until it is at close range
Directional control	Electrical microstimulation of SC evokes orienting movements of head and pinna SC may have a role in orienting flight musculature 3-D neurons of SC are involved in coupling of range axis to directional hearing mechanisms	As the bat flies in pursuit, the aim of its head and the axis of its directional hearing are maintained on the moving insect target
Vocal control	Electrical microstimulation of SC elicits vocalizations coupled with head and pinna movements	The bat processes echo information, which then guides vocalization properties and head and pinna movements
Sonar emissions:		
Pulse duration	2.7 ± 1.0 msec (1.11–7.00 msec)	Typically 2–5 msec
Repetition rate	15.4 ± 5.5 sounds/sec (8.1–56.9 sounds/sec)	10–50 sounds/sec
Frequency of first harmonic	Sweeping from 50 kHz (± 4.3 kHz) to 23.7 kHz (± 4.8 kHz)	Sweeping from 50 kHz to 25 kHz

^aWithin this column, data are given as mean \pm SD.

^bBehavioral information is from Webster and Brazier (1965) and Kick and Simmons (1984).

the general principles guiding the functional organization of the vertebrate midbrain.

Acknowledgments

This work was supported by a Whitehall Foundation Grant and an NSF Young Investigator Award to C.F.M. and a Sackler Programme Fellowship to D.E.V. We thank R. Iannucci for research support, and A. Grossetête, A. Huang, R. Iannucci, D. Rios, G. Sheen, L. Taft, J. Wadsworth, and M. Zagaeski for technical assistance with the experiments summarized in this chapter.

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