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REVIEW

Adaptive mechanisms underlying the bat biosonar behavior

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Abstract For survival, bats of the suborder Microchiropetra emit intense ultrasonic pulses and analyze the weak returning echoes to extract the direction, distance, velocity, size, and shape of the prey. Although these bats and other mammals share the common layout of the auditory pathway and sound coding mechanism, they have highly developed auditory systems to process biologically relevant pulses at the expense of a reduced visual system. During this active biosonar behavior, they progressively shorten the pulse duration, decrease the amplitude and pulse-echo gap as they search, approach and finally intercept the prey. Presumably, these changes in multiple pulse parameters throughout the entire course of hunting enable them to extract maximal information about localized prey from the returning echoes. To hunt successfully, the auditory system of these bats must be less sensitive to intense emitted pulses but highly sensitive to weak returning echoes. They also need to recognize and differentiate the echoes of their emitted pulses from echoes of pulses emitted by other conspecifics. Past studies have shown the following mechanical and neural adaptive mechanisms underlying the successful bat biosonar behavior: (1) Forward orienting and highly mobile pinnae for effective scanning, signal reception, sound pressure transformation and mobile auditory sensitivity; (2) Avoiding and detecting moving targets more successfully than stationary ones; (3) Coordinated activity of highly developed laryngeal and middle ear muscles during pulse emission and reception; (4) Mechanical and neural attenuation of intense emitted pulses to prepare for better reception of weak returning echoes; (5) Increasing pulse repetition rate to improve multiple-parametric selectivity to echoes; (6) Dynamic variation of duration selectivity and recovery cycle of auditory neurons with hunting phase for better echo analysis; (7) Maximal multiple-parametric selectivity to expected echoes returning within a time window after pulse emission; (8) Pulse-echo delay-sensitive neurons in higher auditory centers for echo ranging; (9) Corticofugal modulation to improve on-going multiple-parametric signal processing and reorganize signal representation, and (10) A large area of the superior colliculus, pontine nuclei and cerebellum that is sensitive to sound for sensori-motor integration. All these adaptive mechanisms facilitate the bat to effectively extract prey features for successful hunting.

Keywords adaptive mechanisms, bat biosonar, behavior

1 Introduction

It was Spallanzani (1793) who first noticed that a bat could fly successfully in total darkness and a blind bat could avoid obstacles as dexterously as a normal one even when its wings had been carefully coated with varnish or when its sense of taste and smell had been removed. He concluded that a bat must be endowed with a sixth sense. Jurine (1798) concluded that a bat's ears rather than eyes are necessary for orientation after he observed that a blind bat could not avoid obstacles after various waxy substances had been introduced into its ears. Although this conclusion was accepted by Spallanzani at his death (1799), the then authoritative zoologist Cuvier (1805) who did not even try to verify Jurine's finding disagreed and maintained that the organs of touch were sufficient to explain the bat's obstacle avoidance phenomena. This tactile hypothesis dominated the view of scientific community until Rollinat and Trouessart (1900) restudied the mystery of bat orientation.

Hahn (1908) made his bats fly between regularly spaced vertical wires with and without their ears plugged and obtained quantitative data on their ability to avoid the wires. He concluded that bats perceive obstacles mainly through sense organs located in their internal ears. In 1912, Maxim contended that a bat can avoid obstacles by detecting returning echoes of low frequency sounds produced by its wingbeats. However, Hartridge (1920) proposed that a bat might use ultrasonic rather than infrasonic signals for orientation. It was Pierce and Griffin

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(1938) who used a device sensitive to high frequency signals to demonstrate that bats emit ultrasonic signals. After scrupulously repeating all the previous experiments, Griffin and Galambos (1941) concluded that bats avoid obstacles by emitting ultrasonic signals and listening to the returning echoes for orientation. This active perceptual process, requiring both generation of sounds and sensory analysis of the returning echoes was termed "echolocation" (Griffin, 1944).

Although echolocating bats and other mammals share the common layout of the auditory pathway and sound coding mechanism, they have highly developed auditory systems to process biologically relevant pulses at the expense of a reduced visual system. In particular, it has a disproportionate tonotopic representation for processing biologically relevant sonar signals (Suga and Jen, 1976; Jen et al., 1989). The bat's echolocation system consists of three parts: audition, vocalization, and orientation (Fig. 1). The "audition" part is responsible for the reception of self-emitted signals, the returning echoes, and signals emitted by other animals. The "vocalization" part produces species-specific air-born signals and the "orientation" part modulates motor activities of different parts of the body to produce a specific flight pattern to catch prey or avoid obstacles. These three parts should work coordinately so that a bat can (1) emit a repertoire of orientation signals and systematically change multiple parameters of the emitted signals during different phases of hunting; (2) have its own ears protected from intense self-emitted signals and yet remain highly sensitive to the returning echoes; and (3) coordinate activities of different groups of muscles for proper acoustic-guided orientation. In short, successful echolocation requires effective signal emission, processing and highly coordinated motor activities.

In order to emit intense ultrasonic signals and remain highly sensitive to the weak returning echoes, a bat requires a specialized laryngeal apparatus and attenuating mechanism. To successfully intercept a prey or negotiate an obstacle demands that the bat to recognize and differentiate the echoes of self-emitted pulses from echoes of pulses emitted by other bats so as to accurately decipher the features of its localized target. Finally, to produce an effective flight pattern during echolocation demands a modulating center or centers that properly integrate and coordinate signal reception with motor execution.

Ever since the discovery of bat biosonar behavior by Griffin and Galambos in 1941, numerous studies have advanced our knowledge on the adaptive mechanisms of this acoustic behavior. Because of the page limitation, the intent of this review article is to describe the adaptive mechanisms underlying the bat biosonar behavior mainly based on the research works that my former coworkers and I have been involved. The work of others is described only as it seems pertinent and essential for the discussion of the present topic.

The adaptive mechanisms underlying the bat successful biosonar behavior can be enumerated as the following.

2 The adaptive mechanisms underlying the bat successful biosonar behavior

2.1 Forward orienting and highly mobile pinnae for effective scanning, signal reception, sound pressure transformation, and mobile auditory sensitivity

In sound localization, an animal utilizes interaural disparity of pressure and arrival time of the stimulus (van Bergeijk, 1962). The importance of these two cues varies among animals because their magnitudes vary with acoustic signal frequency as well as the acoustic properties and size of the head and pinnae of the animal. Depending upon species, the somewhat horn-shaped pinnae of the bat may be simple or complex, large or small with varied degrees of mobility.

Echolocating bats which use ultrasonic signals for acoustic orientation generally have a relatively small head and their echolocation system is highly directional (Shimozawa et al., 1974). As such, conjunctive or disjunctive movements of the pinna during echolocation probably would not greatly change the travel distance for echoes, but they would certainly change the relationship between interaural pressure difference and angle of incidence of the echo source. However, any movement of their forward orienting pinnae would help them reject background clutter. Their upside-down hanging would seem not only to facilitate echo scanning in wide angle but also to conserve energy during take-off for prey capture.

The importance of pinnae position to the success of echolocation has been shown in many studies. For example, the shape and pinna position contribute importantly to the creation of directionality of sound pressure transformation at the pinna of the bat (Jen and Chen, 1988). As shown in Fig. 2, the head and pinna of three different species of bat (*Eptesicus fuscus, Carollia* sp. and *Pteronotus parnellii parnellii*) have different shapes, sizes and orientation. As such, the pattern of iso-pressure contours of directionality of sound pressure transformation at the head and pinna for the same signal frequency shows a species-specific difference.

Other behavioral studies have shown that a displacement of pinnae from their normal position affects a bat's ability to avoid obstacles (Griffin, 1958; Jen and McCarty, 1978a, b; Wieder and Jen, 1979; Jen et al., 1980a, b; Sun et al., 1987b), to perceive the vertical position of a target (Lawrence and Simmons, 1982; Wotton et al., 1996) and to detect presented stationary and moving targets (McCarty and Jen, 1983). Furthermore, electrophysiological studies have shown that auditory neurons typically display maximal directional selectivity to a sound presented at a specific point of the bat frontal auditory space. This point

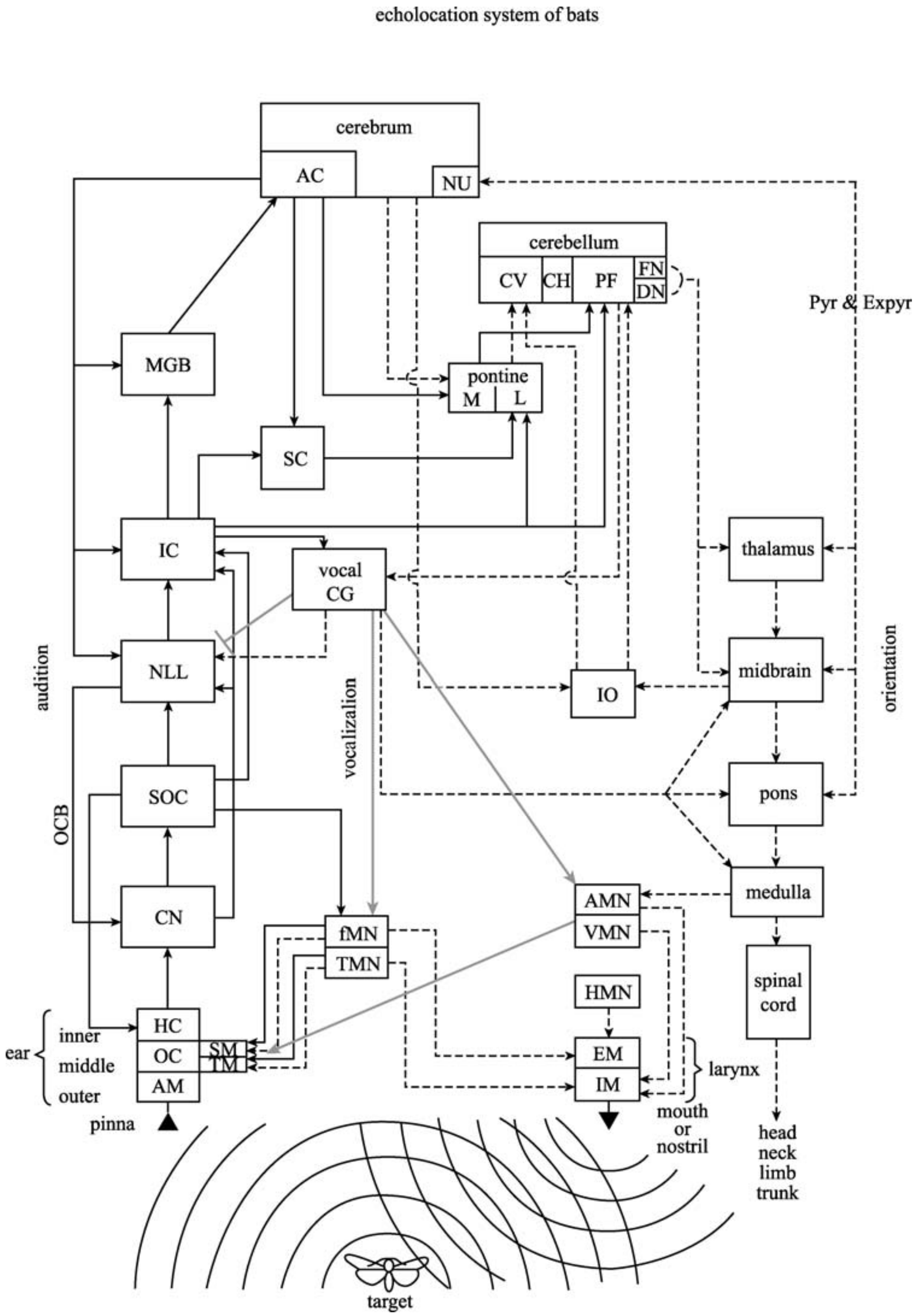

Fig. 1 Simplified schematic diagram of bat echolocation system. Solid lines represent the auditory system and dashed lines represent the motor system. AC: auditory cortex; AM: auditory meatus; AMN: ambiguous motor nucleus; CG: central gray mailer; CH: cerebellar hemisphere; CN: cochlear nucleus; CV: cerebellar vemtis; DN: dentate nucleus; EM: extrinsic muscle; Expyr: Extrapyramidal system; FMN: facial motor nucleus; FN: fastigial nucleus; HC: hair cell; HMN: hypoglossal motor nucleus; IC: inferior collculus: IM: intrinsic muscle; IO: inferior olive; L: lateral; M: medial; MGB: medial geniculate body; NLL: nucleus of lateral lemniscus; NU: nucleus; OC: ossicular chain; OCB: olivocochlear bundle; PE: paraflocculus; Pyr: pyramidal system; SM: stapedius muscle; SC: superior colliculus; SOC: superior olivary complex; TM: tensor tympani muscle; TMN: trigenminal motor nucleus; VMN: vagus motor nucleus (From Jen, 1982). The gray lines show the peripheral mechanical and central neural attenuation of intense emitted pulses during vocalization (see text for details).

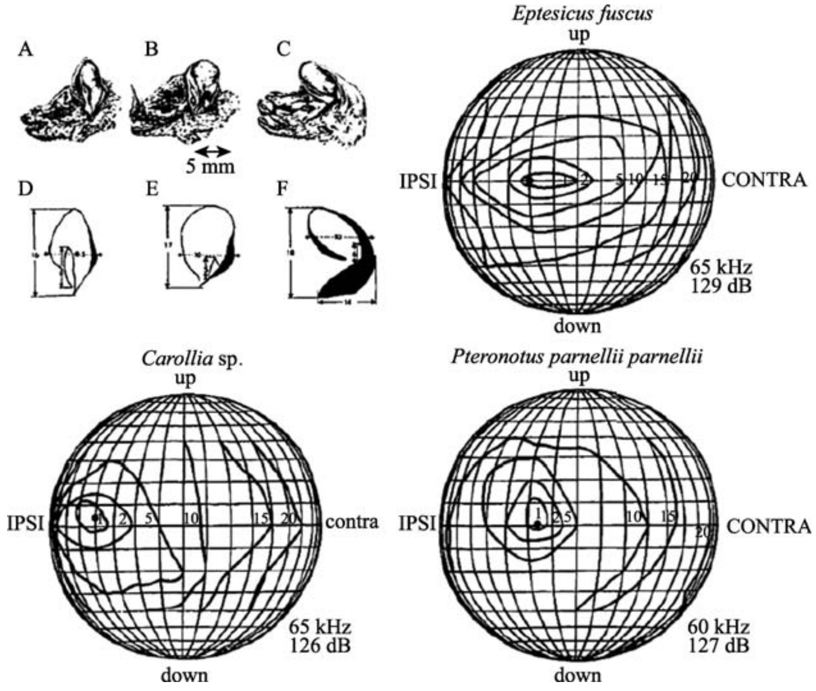

Fig. 2 A lateral view of the head and pinna of an *Eptesicus fuscus* (A), a *Carollia* sp. (B) and a *Pteronorus parnellii parnellii* (C). The dimensions of the pinna and tragus of each bat are shown in D, E and F. Note the whole tragus of *Carollia* sp. and *Pteronolus parnellii parnellii* is not visible. Representative iso-pressure contours of directionality of sound pressure transformation at the head and pinna of these three bat species as measured with 65 kHz tonal frequencies. Each solid dot represents the point of the maximal sound pressure which is shown below the frequency. Each circumscribed or uncircumscribed solid line represents the boundary of 1, 2, 5, 10, 15, 20 or 25 dB optimal area (From Jen and Chen, 1988).

of maximal directional selectivity greatly depends on the orientation of the bat's pinna (Jen and Sun, 1984; Jen and Wu, 1993). When one or both pinnae bend downward, the point of maximal directional selectivity generally shifts downward in the frontal auditory space (Figs. 3A *vs* B, C, D). As such, the representation of the frontal space in the midbrain auditory nucleus, the inferior colliculus (IC), also varies with the pinna position (Sun and Jen, 1987; Jen et al., 1991; Fig. 4). Thus, all these behavioral and electrophysiological studies suggest that pinna characteristics such as position, convolution and movement play an important role during localization of an echo source.

2.2 Insectivorous bats detect moving targets more successfully than stationary ones

The bat ultrasonic pulses are produced by the larynx and have simple frequency-to-time courses. According to the frequency content of the ultrasonic pulses, insectivorous bats typically emit three types of orientation sounds (Neuweiler, 1990, 2003). They are frequency modulated (FM) signals, signals containing a constant frequency (CF) component plus a short FM component and noise bursts or clicks. Bats using these different signals for hunting can be called FM, CF-FM and noise or click bats. The FM bats hunt insects on the wing and typically emit intense 0.5–4.0 msec multiple harmonics FM pulses that sweep downward about one octave in frequency when approach and intercept a prey. However, they often emit longer and only shallowly modulated signal when they search for prey. The CF-FM bat often hunt insects within or close to dense vegetation and typically emit 2.0–60 msec multiple harmonics CF pulses that are terminated with brief 0.8–2.0 msec downward FM sweep at 15%–20% in frequency. The noise or click bats generally emit faint brief signals over a broad frequency band to pick up prey from substrates or visit flowers and fruiting vegetation.

During hunting, an insectivorous bat always moves its head and/or its pinnae to scan its environment such that the returning echoes would always appear moving toward the bat whether they are reflected from moving or stationary targets. For this reason, the bat would seem to concentrate more intently on moving objects during hunting. Indeed, a behavioral study has shown that the CF-FM bat, *Pteronotus parnellii parnellii*, only attack insects or mechanical models of insects with fast wing movements (Goldman and Henson, 1977). Other studies have shown that under a two-choice psychophysical procedure, a trained FM bat, *Eptesicus fuscus*, detects a moving or revolving target more successfully than a stationary one,

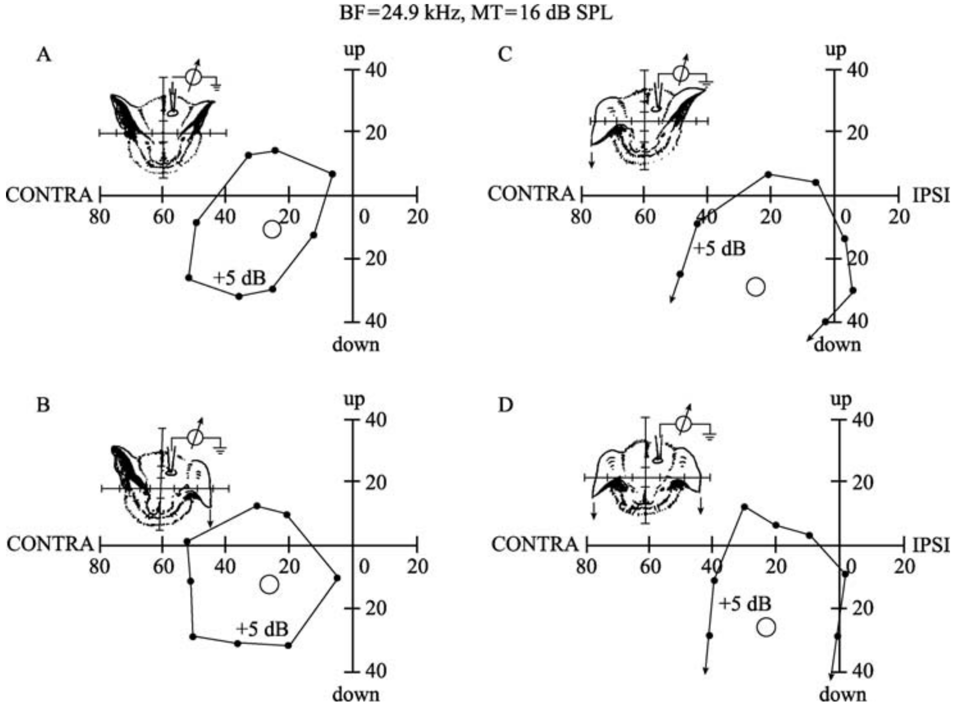

Fig. 3 Spatial response centers (unfilled circles) and 5·dB spatial response areas of one representative inferior collicular neurons measured under four different pinna positions (see bat pictures). CONTRA and IPSP: contralateral and ipsilateral to the recording site. Up and down: upper and lower portion of the bat's frontal auditory space (From Jen and Sun, 1984).

even under monaurally plugged condition (McCarty and Jen, 1983; Jen and Gold, 2004). The trained *Eptesicus fuscus* also approaches a revolving target more frequently than a stationary one when both targets were randomly and simultaneously presented in two directions of a three-ramp platform (Zhang and Jen, 1984). Furthermore, when the FM bats, *Myotis lucifugus* and *Eptesicus fuscus*, as well as the CF-FM bats *Pteronotus parnellii parnellii*, are made to negotiate an array of stationary and moving wires, they negotiate moving wires more successfully than stationary ones although they have different flight patterns (Jen and McCarty, 1978a, b; Jen et al., 1980a, b; Jen, 1982a; Jen and Kamada, 1982; Fig. 5).

The fact that bats detect moving objects more successfully than stationary ones is probably associated with the fact that insectivorous bats rely on moving prey for survival, and they apparently would concentrate more intently on moving objects while hunting. Electrophysiological studies have shown that the two midbrain nuclei, the inferior and superior colliculi, contain neurons that are

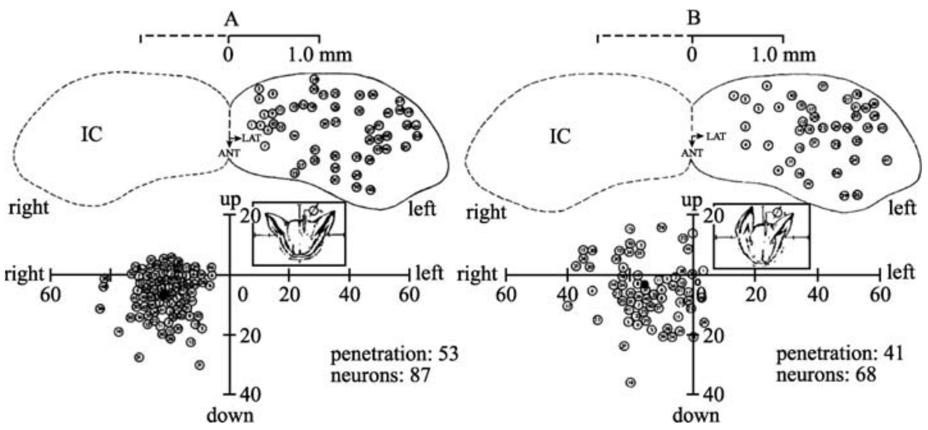

Fig. 4 The auditory space representation in the inferior colliculus (IC) of *Eptesicus fuscus* measured in the normal (A) and monaural vertical (B) pinna position. The locations of electrode penetrations into the left IC and the spatial response centers of recorded IC neurons measured at the right frontal auditory space are shown. The solid circle represents the mean spatial response center (From Sun and Jen, 1987).

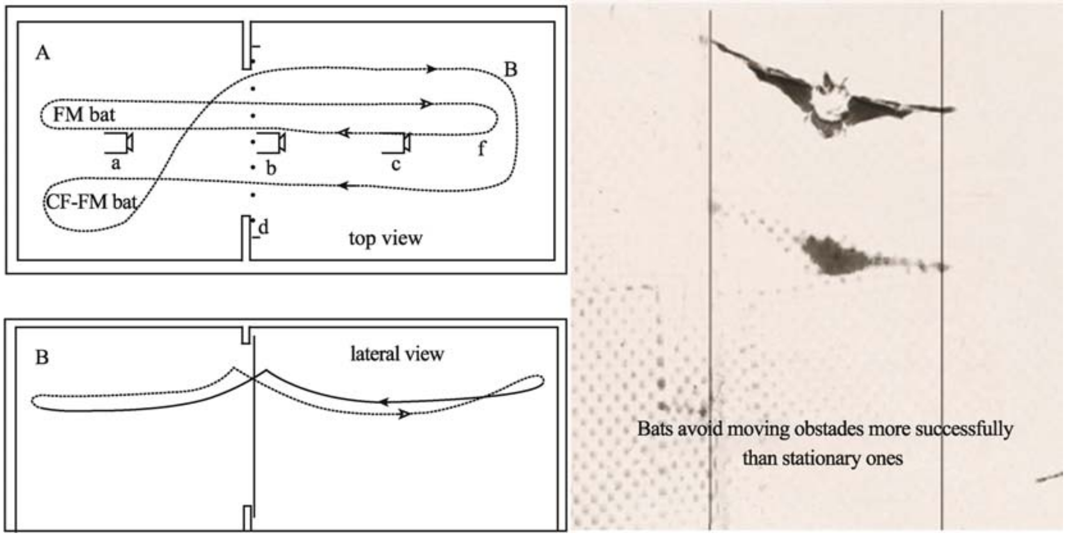

Fig. 5 Left: A top and lateral view of the obstacle-avoidance flight room showing the positions of three microphones (a, b, and c) relative to the array of obstacles (d) and the flight path (dotted line, e) of a CF-FM bat, *Pteronotus p. parnellii* and an FM bat, *Eptesicus fuscus* (From Jen and Kamada, 1982). Right: A photo showing a little brown bat, *Myotis lucifugus*, negotiating vertically-spaced wires in a flight chamber whose walls are covered with convoluted polyurethane.

particularly sensitive to sound source moving in a specific direction (Schlegel et al., 1988; Jen et al., 1993).

2.3 Coordinated activity of highly developed laryngeal and middle ear muscles during pulse emission and reception

Sound emission in most mammals results from the momentary opening of tensed vocal cords owing to the buildup of the air pressure during the exhalation phase of respiration. Energy for sound emission comes from the lungs. Thus, the intensity of the sound is closely related to the force of contracting chest muscles (Kaplan, 1970). The laryngeal apparatus of echolocating bats possesses certain specialized features for emission of ultrasonic signals. Anatomical studies of the larynx of bats revealed disproportionate development of laryngeal muscles (LM), the cricothyroid muscle (CTM) in particular. The CTM of the bat possesses a well-developed sarcoplasmic reticulum and tubulofilamentous fasciculi which may facilitate the fast action of the CTM for emission of ultrasonic signals at high repetition rates (Cho et al., 1972; Revel, 1962). The CTM, which is innervated by a branch of the vagus nerve, the superior laryngeal nerve (SLN), regulates the tension of the vocal membranes during the exhalation of a bat to produce the intense ultrasonic signals (Novick and Griffin, 1961). Suthers and Fattu (1973) showed that the CTM contracted just prior to each vocalization and relaxed during phonation. They suggested that CTM relaxation might gradually decrease the tension of the vocal membranes and thus create the downward FM sweep of the orientation signals. In the CF-FM bat, such as *Rhinolophus ferrum equinum*, unilateral denervation of the SLN reduced the CF frequency by 4–6 kHz, but bilateral denervation reduced the CF frequency by as much as 30 kHz and introduced several strong harmonics into its orientation sounds (Schuller and Suga, 1976).

In addition to possessing a specialized laryngeal apparatus for ultrasonic pulse emission, a bat also has two highly developed middle ear muscle (MEMs, stapedius muscle, SM and tensor tympanic muscle, TM) (Henson, 1961, 1965, 1970). These two groups of muscles (LM and MEM) discharge action potentials not only prior to sound emission (vocal LM and MEM activity) but also during acoustic stimulation (acoustic LM and MEM reflex activity)(Jen and Suga, 1976; Jen and Ostwald, 1977; Jen et al., 1978). Electrical stimulation of the CTM elicits discharge from the two MEMs but not vice versa. The LM becomes active prior to the MEM during vocalization but becomes active after the MEM during sound reception (Fig. 6). Apparently, these two groups of muscles are activated in a coordinated manner not only by the nerve impulses originating from the vocalization centers but also by those from the auditory system.

2.4 Mechanical and neural attenuation of intense emitted pulses to prepare for reception of weak returning echoes

The insectivorous bat such as *Myotis lucifugus* emits intense signals (110–120 dB SPL when monitored at 8 cm in front of the bat's mouth) for echolocation. If such

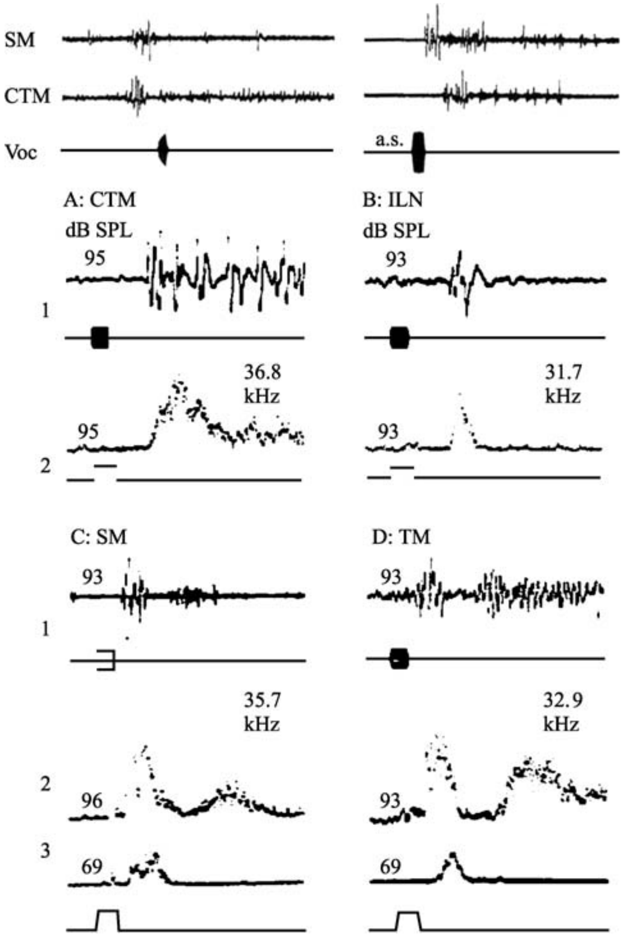

Fig. 6 The discharge of the stapedius (SM) and cricothyroid muscles (CTM) of the little brown bat, *Myotis lucifugus*, during pulse emission (voc) and acoustic stimulation (a.s.). Responses of the CTM, SM, the inferior laryngeal nerve (ILN) and tensor tympani muscle (TM) to 4.0 msec tone bursts. The 2 and 3 represent the average of responses to 32 stimuli delivered at 1.5 bursts/s (From Jen and Suga, 1976; Jen et al., 1978).

intense signals directly impinge upon the bat's ears, detection of faint returning echoes would be greatly impaired. Because bats utilize the time delay between the emitted pulse and returning echo to determine the target distance (echo ranging), stimulation by the self-emitted pulses is probably important in controlling vocalization and in echo ranging. However, this self-stimulation need not be unnecessarily intense and should be considerably attenuated for successful prey capture.

Wever and Vernon (1961) reported that the pinnae and the related aural protuberance of *Myotis Iucifugus* closed the external auditory meatus when an intense sound was delivered to the bat. This mechanical shielding attenuated the intensity of signals above 1 kHz between 40 and 60 dB. In addition, muscular and neural attenuation of intense emitted signals can be as large as 35–45 dB (Suga and Jen, 1975; Suga and Schlegel, 1972).

Muscular attenuation is performed by the two MEMs, which begin to contract prior to pulse emission and reach the maximum contraction just before emission. Such MEM contraction synchronized with sound emission attenuates the self-emitted signals by 17–25 dB (Henson, 1965; Suga and Jen, 1975; Fig. 7). Most of the MEM attenuation of emitted pulses is due to the contraction of the stapedius muscle (SM). The MEM can theoretically contract at a rate of 150 pps without overlap and can effectively attenuate the rapid emission of the orientation signals but not the echoes. Such MEM activity synchronized with vocalization appears to be well suited for FM bats which use brief (2–5 msec) signals and regulate the pulse duration to prevent pulse-echo overlap during echolocation.

In the CF-FM bat, such as *Pteronotus parnellii parnellii*, the orientation signal is usually long (6–28 msec) so that pulse-echo overlap is unavoidable during echolocation (Novick, 1971). The MEM contract maximally during emission of the CF component and relaxation occurs during the terminal FM sweep (Suga et al., 1974). Attenuation of emitted signals by MEM contraction is 20–25 dB for signal frequencies below 57 kHz but is poor for signals with frequencies above 60 kHz (Pollak and Henson, 1973; Suga et al., 1974). Since the auditory system of this bat is sharply tuned at 61 kHz (Suga et al., 1974, 1975; Suga and Jen, 1976, 1977), the CF-FM bat can still receive the Doppler-shifted echoes at about 61 kHz even during periods of pulse-echo overlap when the MEM strongly contract.

Central neural attenuation operates in synchrony with vocalization reduces the sound-evoked activity of the nucleus of the lateral lemniscus by about 15–20 dB (Suga and Schlegel, 1972; Suga and Shimozawa, 1974). During signal emission, the vocalization center(s) either sends inhibitory impulses to suppress the sound-evoked activity in the nucleus of the lateral lemniscus or activates the descending corticofugal system which in turn suppresses the activity of the ascending auditory system.

In summary, the vocalization center sends excitatory impulses to activate discharges from both the LM and MEMs and inhibitory impulses to suppress the discharge in the nucleus of the lateral lemniscus during pulse emission (Fig. 1, grey lines). As such, these peripheral and central neural attenuation mechanisms could attenuate the 110–120 dB self-emitted pulses by 35–45 dB. This amount of attenuation plus the atmospheric attenuation would certainly prevent the bat's ear from overstimulation during pulse emission. As a result, the bat auditory system could remain highly sensitive to process the weak returning echoes for successful prey capture.

2.5 Increasing pulse repetition rate improves multiple parametric echo selectivity

Insectivorous bats such as the big brown bat, *Eptesicus fuscus*, progressively shorten duration, lower frequency,

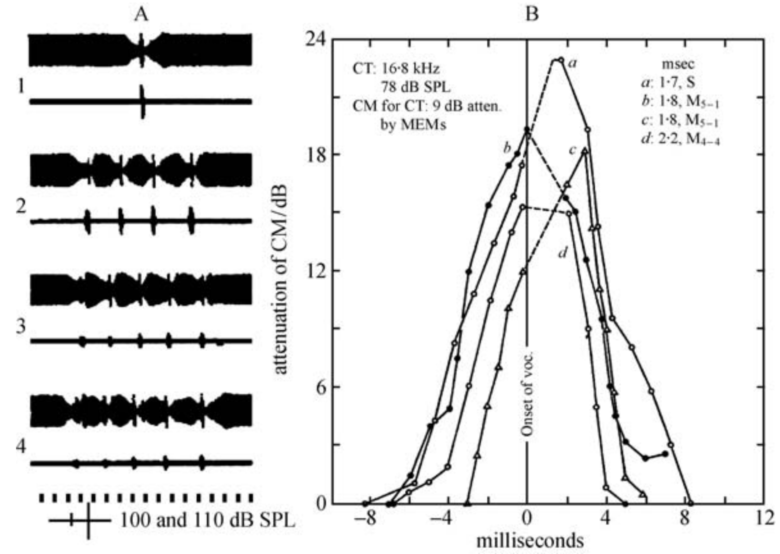

Fig. 7 A: The time course of the vocal middle ear muscles (MEM) contraction of *Myotis lucifugus*. The cochlear microphonic response (CM) evoked by a continuous tone (CT) of 16.8 kHz and 78 dB SPL (upper trace) is transiently attenuated by the MEM contraction when the bat emits orientation sounds (lower trace). In the upper trace, the CM evoked by self-vocalized sounds is also clearly recognizable. At the bottom, 5 msec time signals and 100 and 110 dB SPL acoustic signals are shown. B: The time course of attenuation of the CM by the vocal MEM contraction. The abscissa represents the time before and after the onset of vocalization in msec and the ordinate represents the amount of attenuation in dB. The emitted sounds for curves *a-d* are single pulse of 1–7 msec (S) and multiple pulses (M) of 1.8–2.2 msec. It should be noted that the CM was attenuated by about 9 dB by the acoustic MEM reflex (From Suga and Jen, 1975).

decrease amplitude and increase repetition rate of emitted pulses as they search, approach, and finally intercept insects or negotiate obstacles (Griffin, 1958; Jen and Kamada, 1982; Simmons et al., 1979; Surlykke and Moss, 2000). Figure 8 shows the pulse emission of a bat during hunting as well as the envelopes and sonagrams of orientation signals emitted by a CF-FM bat, *Pteronotus parnellii parnellii* and an FM bat, *Eptesicus fuscus* during different phases of negotiating an array of wires (Jen and Kamada, 1982). During the search phase, the pulse repetition rate is about 10–20 pps with long pulse duration (10–20 msec). As the bat approaches the target, the pulse duration shortens (4–6 msec) and the repetition rate increases to about 30–40 pps. When the bat intercepts the prey or negotiates the wires during the terminal phase, the pulse duration further shortens (1.5–2 msec) and the repetition rate increases to about 90–150 pps.

Presumably, the increase in pulse repetition rate is to obtain maximal information from the increasing number of echoes about the rapid changes in the target or obstacle position. The shortening of pulse duration is to avoid the overlap of the outgoing sounds and returning echoes (Novick, 1971). Because of different pulse duration emitted during hunting, such pulse-echo overlap generally would not occur during prey capture for FM bat like *Eptesicus fuscus* but would occur for the CF-FM bat like *Pteronotus parnellii parnellii* (Novick, 1971; Schnitzler and Henson, 1980). However, in the latter, pulse-echo overlap only occurs in the CF portion but not in the terminal FM portion of the orientation sounds. Finally, the generally lowering of the frequency in the terminal phase is conceivably due to the inability of the bat laryngeal muscles to reach its full extent of each contraction and relaxation cycle at a high pulse repetition rate.

Although variation in the pulse parameter throughout the entire course of hunting would allow the bat to obtain maximal information about the prey, this dynamic variation in multiple parameters of emitted pulses also predicts that analysis of an echo parameter by bats would be inevitably affected by other co-varying echo parameters. Indeed, past studies have shown that the rate-amplitude functions of inferior collicular neurons of *Eptesicus fuscus* change from one type to another with pulse duration (Zhou and Jen, 2002a). Increasing pulse repetition rate elevates the minimum threshold and lengthens the response latency of most collicular neurons (Chen and Jen, 1994; Jen and Chen, 1998).

In the real world, natural sounds such as vocal communication sounds of many animal species typically occur as sequential sound pulses. Therefore, the response magnitude of auditory neurons to a sound pulse would be affected when the sound pulse is preceded and succeeded by other sound pulses (i.e., forward and backward masking). As evident in a study, the response magnitude of collicular neurons is often larger when stimulated with a single sound pulse than when stimulated with the same sound pulse presented in temporally patterned pulse trains (Moriyama et al., 1994). Furthermore, the response size of collicular neurons progressively decreases with sequentially presented sound pulses (Hou et al., 1992; Pinheiro et

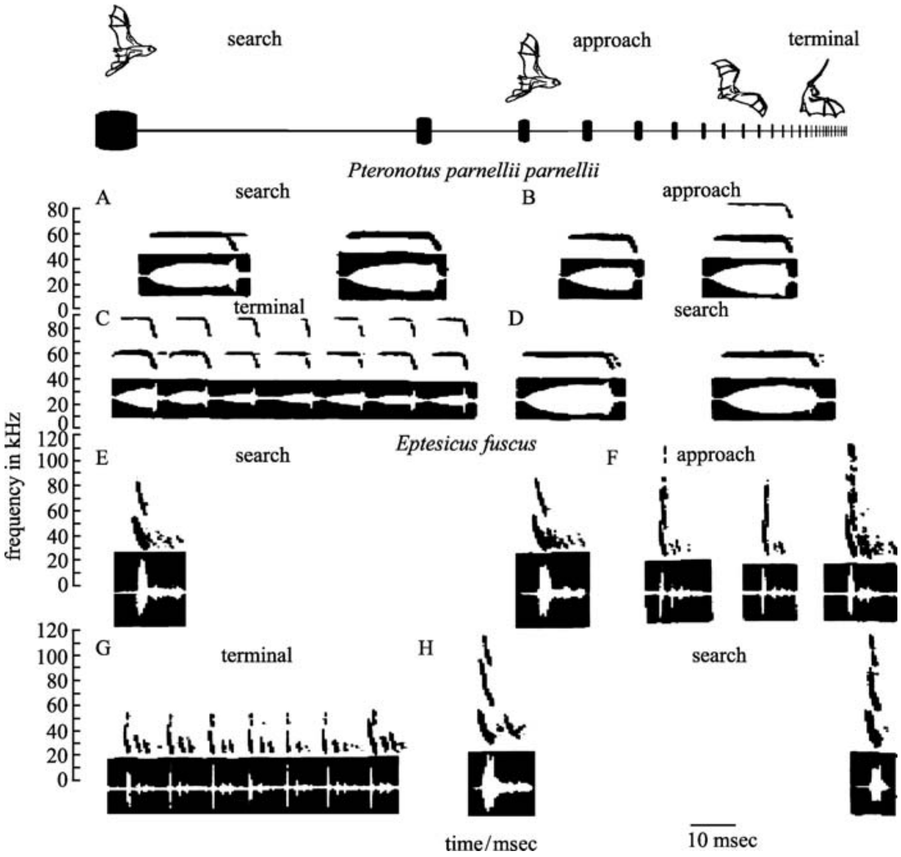

Fig. 8 A cartoon showing the variation in the pulse emission of a bat throughout the entire course of hunting. A–H: Representative envelopes and sonagrams of orientation signals emitted by *Pteronotus p. parnellii* and *Eptesicus fuscus* respectively during different phases of negotiating an array of wires (From Jan and Kamada, 1982).

al., 1991; Jen et al., 1993, 2001; Moriyama et al., 1994; Wu and Jen, 1995a, 1996; Wu et al., 1996; Lu et al., 1997, 1998; Jen and Zhou, 1999; Zhou and Jen, 2002b).

When stimulated with temporally patterned pulse trains at varied pulse repetition rates, the multiple-parametric selectivity (amplitude, direction, duration and frequency) of most collicular neurons progressively improves with pulse repetition rate (Jen and Zhou, 1999; Wu and Jen, 1995b, 1996; Jen et al., 2001, 2002; Zhou and Jen, 2002b, 2006). As such, there is an improvement of the sharpness of directional sensitivity curve (i.e. decreasing azimuth range, AR), frequency tuning curves (i.e. increasing Qn values) and rate-intensity function (i.e. decreasing DR and increasing slope) of collicular neurons with increasing pulse repetition rate (Fig. 9).

Regarding the pulse parameter of duration, auditory neurons that discharge maximally to a particular duration (the best duration, BD, Fig. 10) have been shown in many animals including frogs (Narins and Capranica, 1980), mice (Brand et al., 2000), rats (Perez-Gonzalez et al., 2006) and bats (Jen and Schlegel, 1982; Pinheiro et al., 1991; Casseday et al., 1994; Ehrlich et al., 1997; Galazyuk and Feng, 1997; Jen and Feng, 1999; Jen and Zhou, 1999; Zhou and Jen, 2001; Jen and Wu, 2006, 2008; Wu and Jen, 2006a, b, 2008b, c). The sound duration to which these neurons are tuned corresponds closely to the behaviorally relevant sounds in these animal species. Presumably, these duration-tuned neurons not only play an important role for bat echolocation but also for sound recognition particularly in human speech and animal communication (Popper and Fay, 1995; Shannon et al., 1995; Covey and Casseday, 1999).

During hunting, duration selectivity plays an essential role for echo duration recognition for bat. The success of prey capture by bats indicates that they can effectively encode progressively shortened echo duration throughout the entire course of hunting (Griffin et al., 1960, 1965). The neural basis underlying this successful recognition of echo duration is supported by our studies which show that the BD of duration-tuned collicular neurons ranged between 1.5 and 10 ms covering the duration of pluses emitted by *Eptesicus fuscus* during different phases of hunting (Jen and Schlegel, 1982; Pinheiro et al., 1991; Jen and Feng, 1999; Jen and Zhou, 1999; Zhou and Jen, 2001; Jen and Wu, 2006, 2008; Wu and Jen, 2006a, b, 2008b). When determined with temporally patterned pulse trains, duration selectivity of collicular neurons also improves with increasing pulse repetition rate (Fig. 10).

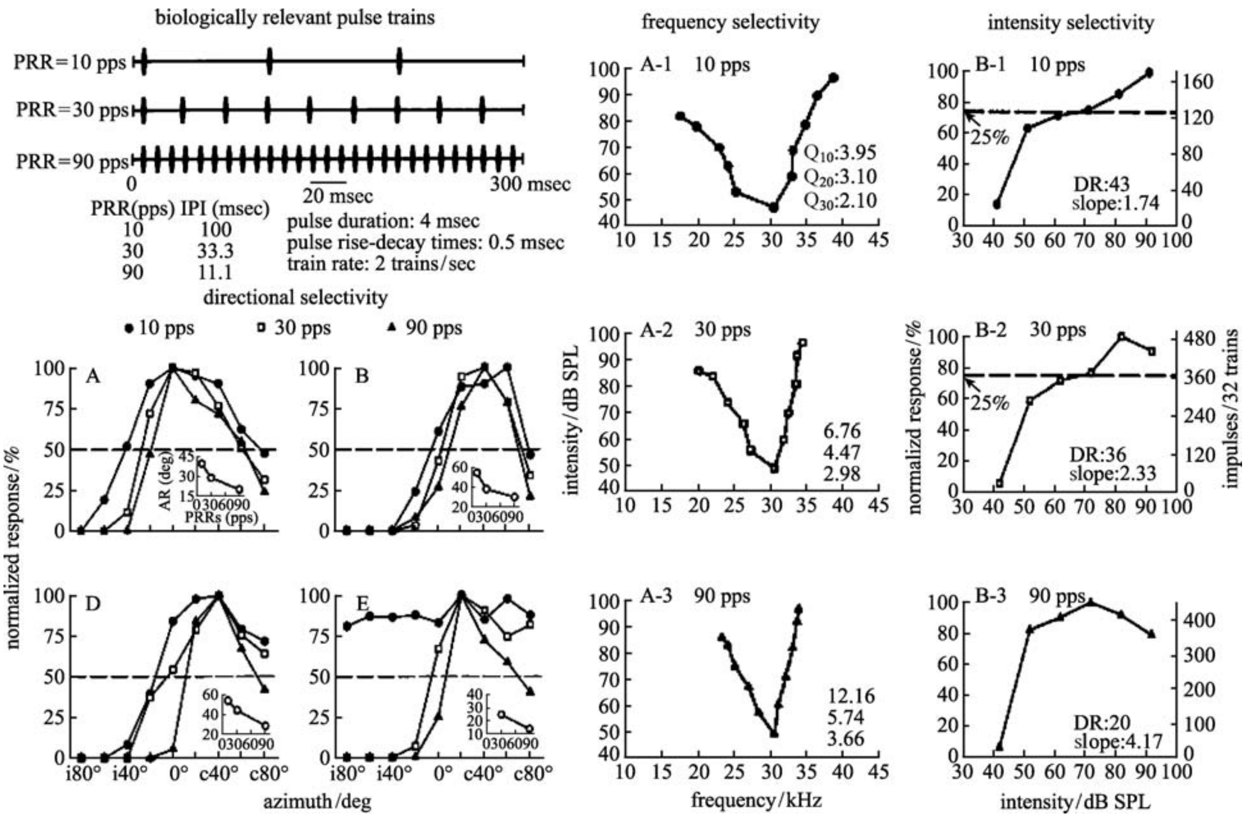

Fig. 9 The three temporally patterned pulse trains used to obtain the directional sensitivity curve, frequency tuning curve and rate-intensity function of inferior collicular neurons of *Eptesicus fuscus*. The sharpness of a directional sensitivity curve is expressed by calculating half of the angular range (AR) at 50% below the maximum of the curve. A directional sensitivity curve with a small AR represents a high sensitivity to change in sound direction. The sharpness of each frequency tuning curve is expressed by Q_n (Q_{10}, Q_{20}, Q_{30}) values which are obtained by dividing the frequency at the lowest threshold (the best frequency, BF) by the bandwidth at 10, 20 and 30 dB above the lowest threshold. A frequency tuning curve with large Qn values represents a high sensitivity to variation in frequency. The dynamic range (DR) of rate-intensity function is defined as the intensity range from 10% below the maximal to 10% above the minimal number of impulses. The slope of the rate-intensity function is obtained by dividing the percent change in the number of impulses within the DR by the DR and expressed in %/dB. A rate-intensity function with a small DR and large (steep) slope represents a high sensitivity to variation in pulse intensity (From Jen et al., 2001; Zhou and Jen, 2002a, b).

All these studies demonstrated that the selectivity of collicular neurons in multiple pulse parameters improves with increasing pulse repetition rate. As a bat increase pulse emission rate throughout the prey approaching sequence during hunting, it can certainly utilize this improvement of multiple parametric echo selectivity to analyze different prey features for successful capture.

2.6 Dynamic variation of duration selectivity and recovery cycle of auditory neurons with hunting phase for better echo analysis

To catch insects, the bat emits intense pulses and listens to greatly attenuated returning echoes in which the gap between the pulse and echo (P–E gap) is always shorter than the gap between two succeeding P–E pairs. As such, the bat's ear is bombarded by pulse-echo pairs throughout the entire course of prey approaching sequence. As a flying bat approaches a prey, echo intensity rapidly increases when the distance to the echo target decreases such that the amplitude difference between the pulse and echo also progressively changes throughout the entire hunting process. Therefore, in the real world the bat analyzes the echo from a series of P–E pairs of unequal amplitude with progressively shortening P–E gap during hunting.

Whereas duration selectivity is important for duration recognition, the recovery cycle, which determines a neuron's ability in response to a succeeding pulse, underlies a bat's ability to detect the returning echoes and to determine the target distance (echo ranging). Since the duration, gap and amplitude between emitted pulse and retuning echo progressively change during different phases

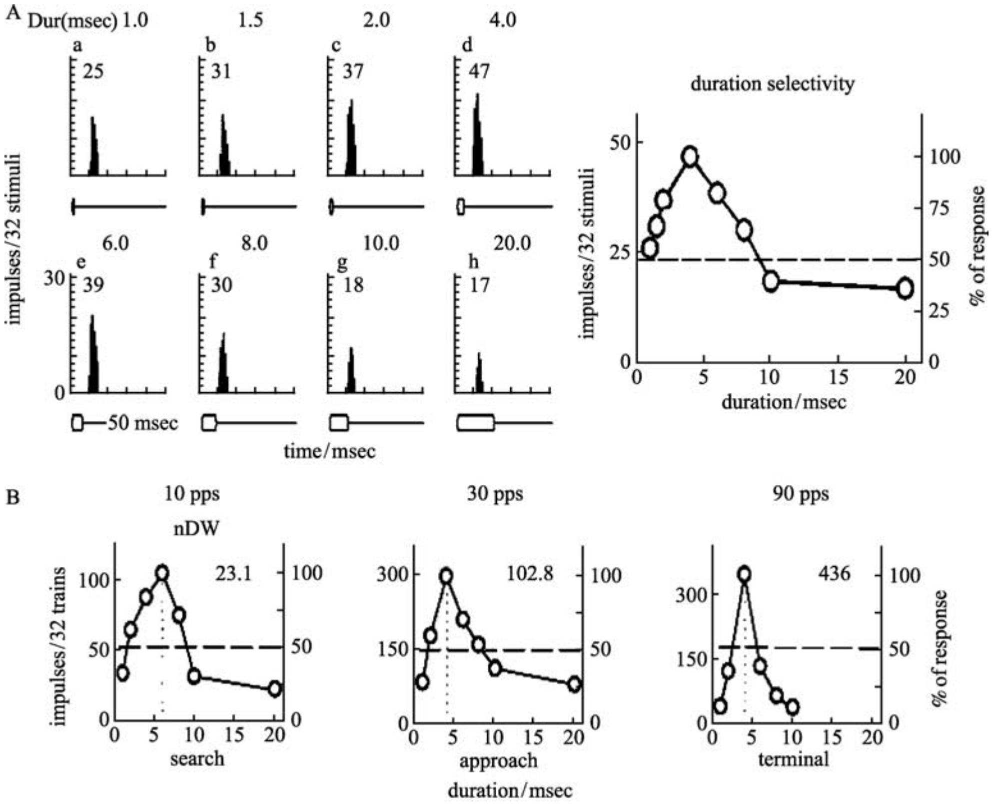

Fig. 10 A: The peri-stimulus-histograms (PST) showing the discharge pattern and duration tuning curve of a representative collicular neuron of *Eptesicus fuscus* obtained with tone bursts at varied duration. B: The neuron's duration tuning curves obtained with three temporally patterned pulse trains at varied pulse repetition rates (pps). The neuron's duration selectivity is expressed by normalized duration-width (nDW) obtained by dividing the maximum of the normalized duration tuning curve by the width of the curve at 50% of maximum. The larger the nDW is, the sharper the duration selectivity is (Wu and Jen, 2006a).

of hunting, a study of variation of echo duration selectivity and recovery cycle of the bat's auditory neurons with biologically relevant P-E pairs is necessary for better understanding of echo duration recognition and echo ranging by bats during hunting.

Recent studies have shown that echo duration selectivity of most collicular neurons of *Eptesicus fuscus* is sharper when determined with P–E pairs than with single pulses based on the variation of sharpness of the duration tuning curves obtained under varied stimulation conditions (Fig. 11). Echo duration selectivity also improves with decrease in duration, gap and amplitude difference of P-E pairs (Wu and Jen, 2006b; Jen and Wu, 2008). As shown in Fig. 12, when studied with three biologically relevant P-E pairs at two different P-E amplitude differences comparable to those occurring during three phases of hunting, the neuron's echo duration selectivity progressively decreased with lengthening of pulse duration and P-E gap as evident by the increase in the echo-BD and duration width (DW) (Fig. 12A, B). The neuron's echo duration selectivity was greater (as shown by a smaller DW) to 4 msec or 10 msec pulse duration at 4 ms or 8 ms P-E gap with 20-dB amplitude difference comparable to the P-E amplitude difference during search and approach phases (Fig. 12Ab, Ac *vs* Bb, Bc, C, D). However, the echo duration selectivity was greater when determined with 1.5 msec pulse duration and 2 msec P-E gap at 10-dB amplitude difference comparable to P-E amplitude difference during the terminal phase of hunting (Fig. 12Ba *vs* Aa, C, D). Clearly, the echo BD became shorter with sharper duration selectivity when obtained with P-E pairs of "terminal" phase at smaller P-E amplitude difference. Conversely, the echo BD became longer with decreased duration selectivity when obtained with P-E pairs of "search" and "approach" phases.

The improvement of echo duration selectivity with shortening of duration, gap and increasing pulse repetition rate is due to increasing strength of GABAergic inhibition (Jen and Wu, 2005; Wu and Jen, 2006a, b). This is supported by the findings that ionophoretic application of GABA increases echo duration selectivity of collicular neurons and the degree of improvement in echo duration selectivity progressively decreases with shortening of pulse duration and P–E gap (Fig. 13). Conversely, the

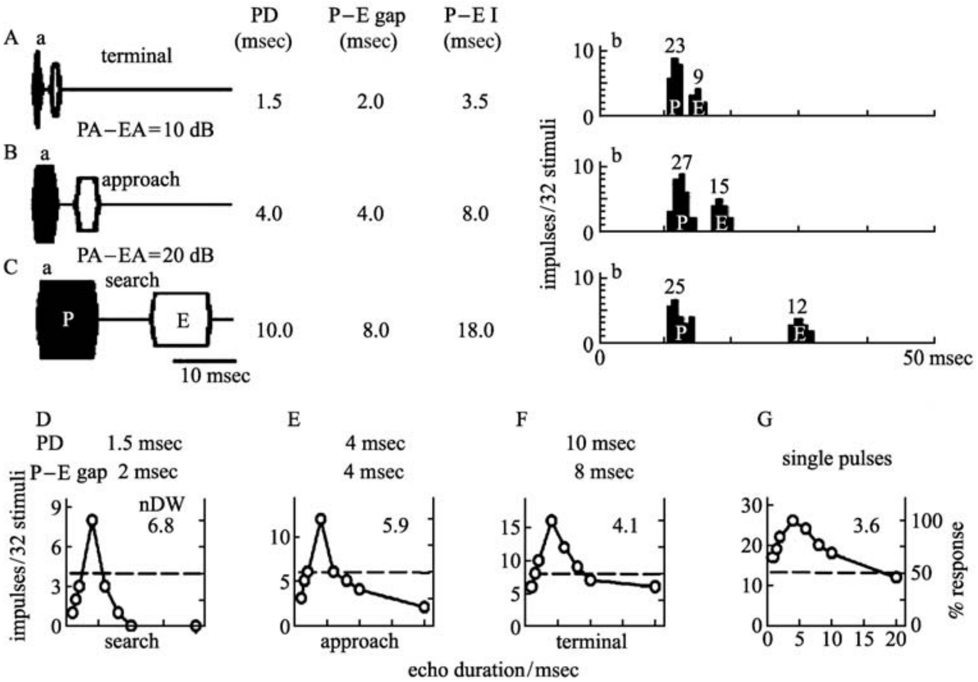

Fig. 11 A–C: Sketches showing the envelope of three biologically relevant pulse–echo (P–E) pairs and the discharge patterns of a collicular neuron of *Eptesicus fuscus* obtained with 32 presentations of three P–E pairs. The neuron's number of impulses in response to each pulse (P) and echo (E) are shown atop. D–G: The duration tuning curves of the collicular neuron obtained with three P–E pairs and single pulses. The neuron has sharper echo duration selectivity when obtained with P–E pairs than with single pulses. Its duration selectivity also increases with the shortening of P–E duration and gap (Wu and Jen, 2006b).

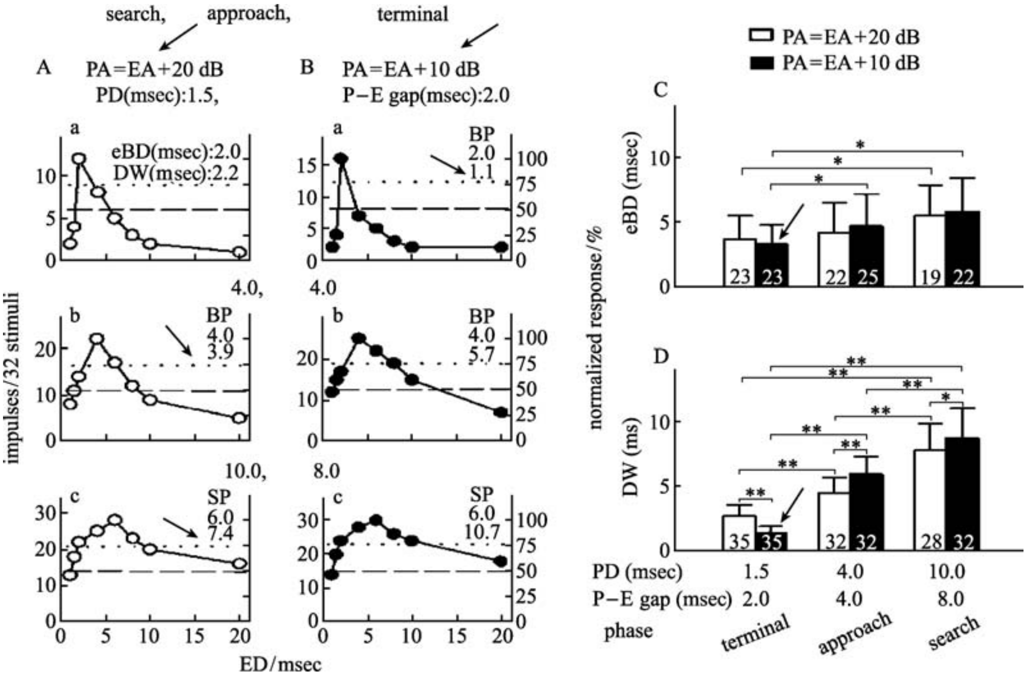

Fig. 12 A, B: The echo duration tuning curves of a collicular neuron of *Eptesicus fuscus* obtained with three biologically relevant P–E pairs that varied in pulse duration and P–E gap at 20-dB (unfilled) and 10-dB (filled) P–E amplitude differences. The sharpness of an echo duration tuning curve is expressed by the width of the curve at 75% of the maximum (duration width, DW). A narrow echo duration tuning curve has a small DW and sharp duration selectivity. C, D: The bar histograms showing the average best echo duration (eBD) and duration width (DW) of collicular neurons (number is shown within each bar) determined with three biologically relevant P–E pairs (shown below) at 20-dB (unfilled) and 10-dB (filled) P–E amplitude differences. **: $P < 0.01$, *: $P < 0.05$ (From Wu and Jen, 2006b).

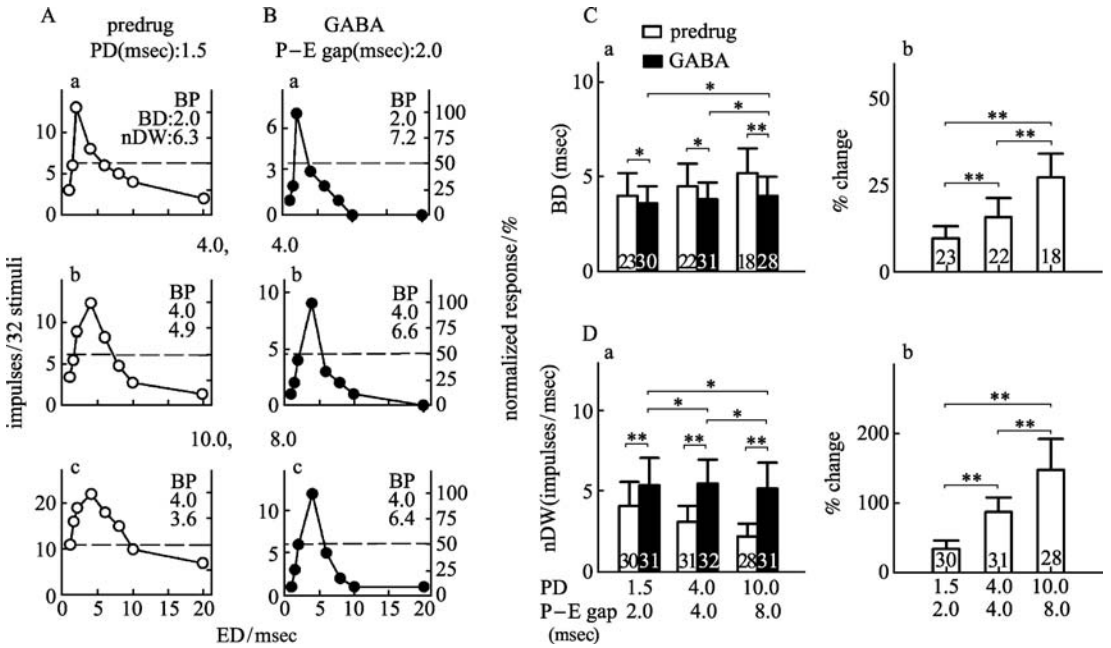

Fig. 13 A, B: Echo duration tuning curves of an IC neuron of *Eptesicus fuscus* determined with three P–E pairs before (predrug, A) and during (B) gamma-aminobutyric acid (GABA) application. Ca, Da: Bar histograms showing the average BD and nDW determined with three P–E pairs of P–E before (predrug, unfilled bars) and during (filled bars) GABA application. Cb, Db: Percent change in the BD and the nDW during the GABA application. **: $P < 0.01$, *: $P < 0.05$ (Wu and Jen, 2006b).

opposite change in the echo duration selectivity was observed during ionophoretic application of bicuculline, an antagonist to GABA.

Because the recovery cycle is one of the two factors (forward masking is the other) underlying a neuron's duration selectivity (Wu and Jen, 2006b), variation of recovery cycle with biologically relevant P-E pairs has been studied for the bat's duration-tuned collicular neurons (Wang et al., 2008, 2010). The recovery cycle of a duration-tuned collicular neuron is studied with a P-E pair at varied P-E intervals and the neuron's echo-elicited response relative to the pulse-elicited response is determined at each interval (Fig. 14). These studies show that the recovery cycle of most duration-tuned collicular neurons varies with biologically relevant P-E pairs. Neurons with short BD recover rapidly when stimulated with P-E pairs with short duration and a small P-E amplitude difference, whereas neurons with long BD recover rapidly when stimulated with P-E pairs with long duration and large P-E amplitude differences. As shown in Fig. 15, the collicular neuron with 1.5 msec BD has the shortest 50% recovery time (dashed line) when stimulated with 1.5 msec P-E pair at 10 dB amplitude difference (B, arrow), while the neuron with 10 msec BD recovered rapidly when stimulated with 10 msec P-E pair at 20 dB amplitude difference (F, arrow). These observations suggest that neurons with different BD would enable the bat to effectively perform recognition of echo duration and echo ranging throughout a target approaching sequence to ensure prey capture.

2.7 Maximal multiple-parametric selectivity to expected echoes returning within a time window after pulse emission

Previous studies have shown that insectivorous bats prepare their auditory system to analyze expected returning echoes for successful orientation and prey capture. For example, the bats greatly attenuate the intense emitted pulses through a peripheral mechanical and a central neural attenuation mechanism during pulse emission so as to maintain the auditory system highly sensitive to weak returning echoes (Henson, 1965; Suga and Schlegel, 1972; Suga and Shimozawa, 1974; Suga and Jen, 1975). They also appear to establish a time window after pulse emission during which echoes are processed for echo ranging (Roverud and Grinnell, 1985; Roverud, 1989). This time window for echo ranging is reset with every emitted pulse either by a signal from the vocalization system or by listening to self-emitted pulse. All these observations suggest that the bat auditory system must be maximally sensitive to pulse parameters of the expected echoes returning within this time window for successful prey capture.

These behavioral observations have been corroborated

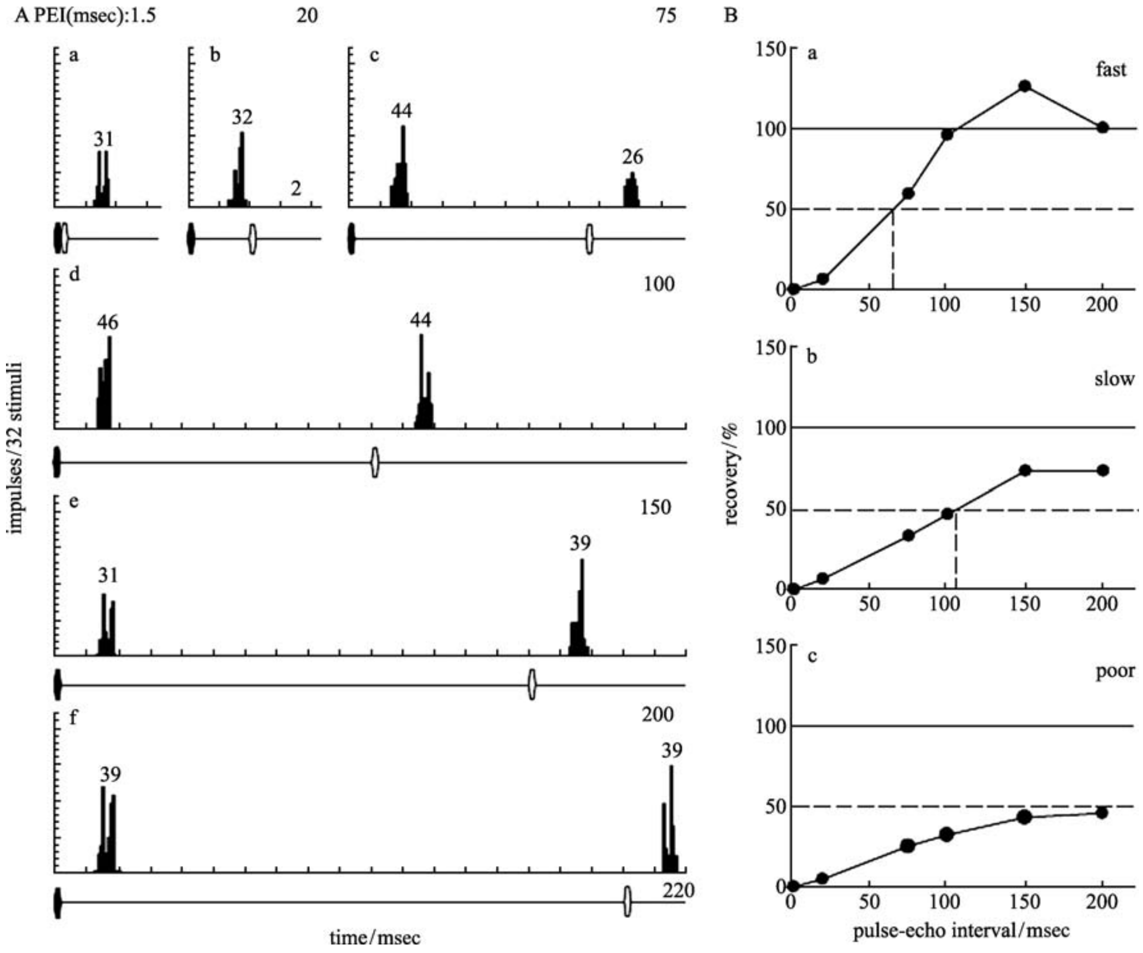

Fig. 14 A: PST histograms showing the discharge pattern of a representative collicular neuron of *Pipistrellus abramus* obtained with a P–E pair (1.5 msec duration, envelope shown below each histogram) at varied P–E intervals (PEI, msec, shown at upper right of each panel). The neuron's number of impulses in response to each P and E shown above each histogram is used to plot its recovery cycle (Ba). B: The fast, slow and poor recovery cycles of three representative IC neurons. The solid and dashed horizontal lines represent 100% and 50% recovery in response. The vertical dashed line represents 50% recovery time (msec) (From Wang et al., 2010).

by recording responses of duration-tuned collicular neurons using single pulses and biologically relevant pulse-echo pulses (Wu and Jen, 2007, 2008a, b). These duration-tuned collicular neurons have the sharpest frequency and amplitude selectivity when stimulated with BD single pulses. These duration-tuned collicular neurons have better echo amplitude and frequency selectivity when the duration of both echo and pulse matches the BD when studied with three biologically relevant P-E pairs (Wu and Jen, 2008c, 2009). As such, the narrowest frequency tuning curve and rate-amplitude function of these neurons is obtained with P-E pairs whose duration matches the BD (Figs. 16 and 17). The echo frequency and amplitude selectivity of these neurons also significantly decreases with shortening of P-E duration and P-E gap. These studies suggest that duration-tuned collicular neurons would enable a bat to improve frequency and amplitude selectivity to the expected echo pulse than to other unexpected echo pulses throughout a target approaching sequence. These studies also indicate that bats can better extract multiple parameters of expected than unexpected echo within the same time window after pulse emission.

2.8 Pulse-echo delay-sensitive neurons in higher auditory centers for echo ranging

During prey capture, most bats, if not all, use FM signals for measuring target range by computing the echo travel time. This echo travel time (i.e. pulse-echo delay) may be analyzed by the interval between the auditory response to the emitted signal and to the echo. Previous studies have shown that in the bat auditory system beginning at the midbrain inferior colliculus and higher auditory centers contains neurons that are preferably or exclusively sensitive to a combination of pulse-echo pairs (i.e. delay-

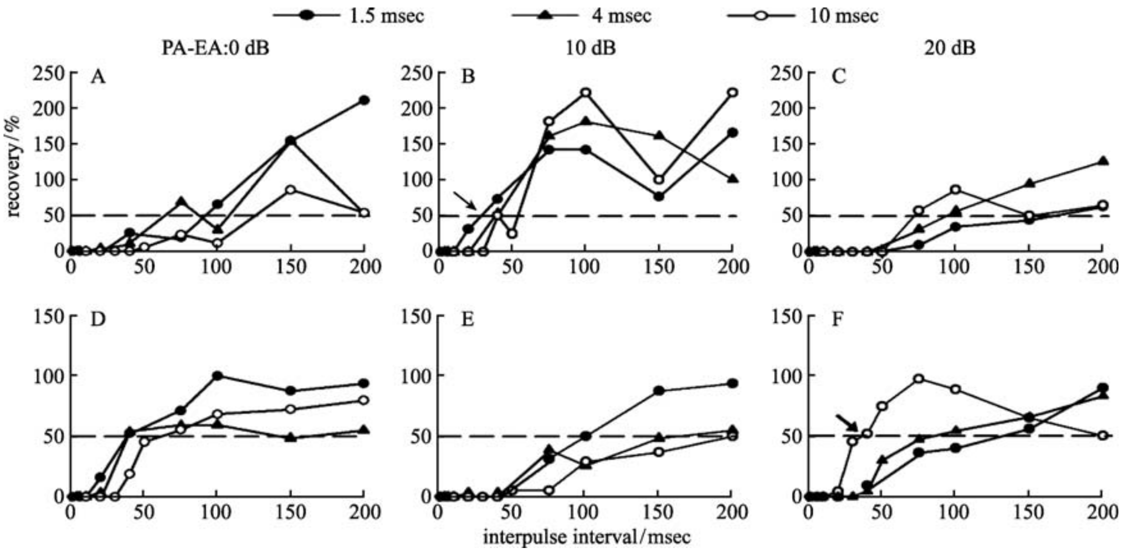

Fig. 15 The recovery cycle of two duration–selective collicular neurons of *Pipistrellus abramus* determined with nine P–E pairs that varied in P–E gap, duration and amplitude differences (PA–EA).The best duration (BD) of these two neurons was 1.5 msec (A–C) and 10 msec (D–F). Note that the neuron with 1.5 msec BD had the shortest 50% recovery time (dashed line) when stimulated with 1.5 msec P–E pair at 10 dB amplitude difference (B, arrow), while the neuron with 10 msec BD recovered rapidly when stimulated with 10 msec P–E pair at 20 dB amplitude difference (F, arrow)(From Wang et al., 2008).

sensitive neurons). These neurons respond poorly or not at all to pulse or echo alone but respond maximally to the pulse-echo delivered at a specific pulse-echo delay (the best delay) (Fig. 18A, B). Because each of delay-sensitive neurons responds only to an echo returning from the appropriate distance, the delay-sensitive neurons have been called ‘‘echo-raging neurons’’ (O’Neill and Suga, 1982; O’Neill, 1987).

Neural circuits underlying the formation of these delay-sensitive neurons may be due to the combination of a long pathway for the pulse-elicited response and a short pathway for the echo-elicited response (Fig. 18C). As such, the echo-sensitive neurons are coincidence detectors (Sullivan, 1982a, b; Olsen and Suga, 1991). Coincidence is most probably achieved by rebound from inhibition elicited by the pulse in which the duration of inhibition varies and corresponds to the best delay of the neurons. While this delay-sensitive or combination-sensitivity is a general feature of auditory reception in all mammals and birds, the echolocating has a large aggregation in midbrain and higher auditory centers (Neuweiler, 2003).

2.9 Corticofugal modulation improves on-going multiple parametric signal processing and reorganizes signal representation

During sensory coding, receptors transduce different stimuli into nervous impulses which transmit along afferent fibers toward the central nervous system. During this ascending signal processing, the brain has the built-in ability to edit and adjust the flow of information that reaches it. This feedback control, which appears to be a common principle across all sensory systems, is executed through efferent pathways. In sound reception, the auditory signal processing has traditionally been explained by neural interactions of divergent and convergent projections within the ascending auditory system through the interplay between excitation and inhibition. However, recent studies have shown that the massive corticofugal system, which is topographically as well-organized as the ascending auditory system, runs in parallel but oppositely to the ascending auditory pathway (Games and Winer, 1988; Huffman and Henson, 1990; Herbert et al., 1991; Saldana et al., 1996; Winer, 2006; Fig. 19).

This descending corticofugal system adjusts and improves ongoing subcortical auditory signal processing by enhancing or suppressing the response of subcortical auditory neurons (Fig. 20A; Sun et al., 1989, 1996; Jen et al., 1998, 2001, 2002, 2003; Zhou and Jen, 2000a, b, 2005, 2007). This corticofugal system sharpens the subcortical auditory sensitivity in multiple parametric domains including direction, frequency and amplitude. For example, the corticofugal system sharpens the direction-dependent frequency selectivity of collicular neurons by expanding the lateral inhibitory area to narrow the excitatory frequency tuning curve (Fig. 20C, D). This modulation of subcortical frequency selectivity is direction-dependent, being greater at contralateral 40° than at ipsilateral 40° (Jen and Zhang, 1999; Zhang et al., 1997, 2000). As all biological meaningful sounds are typically

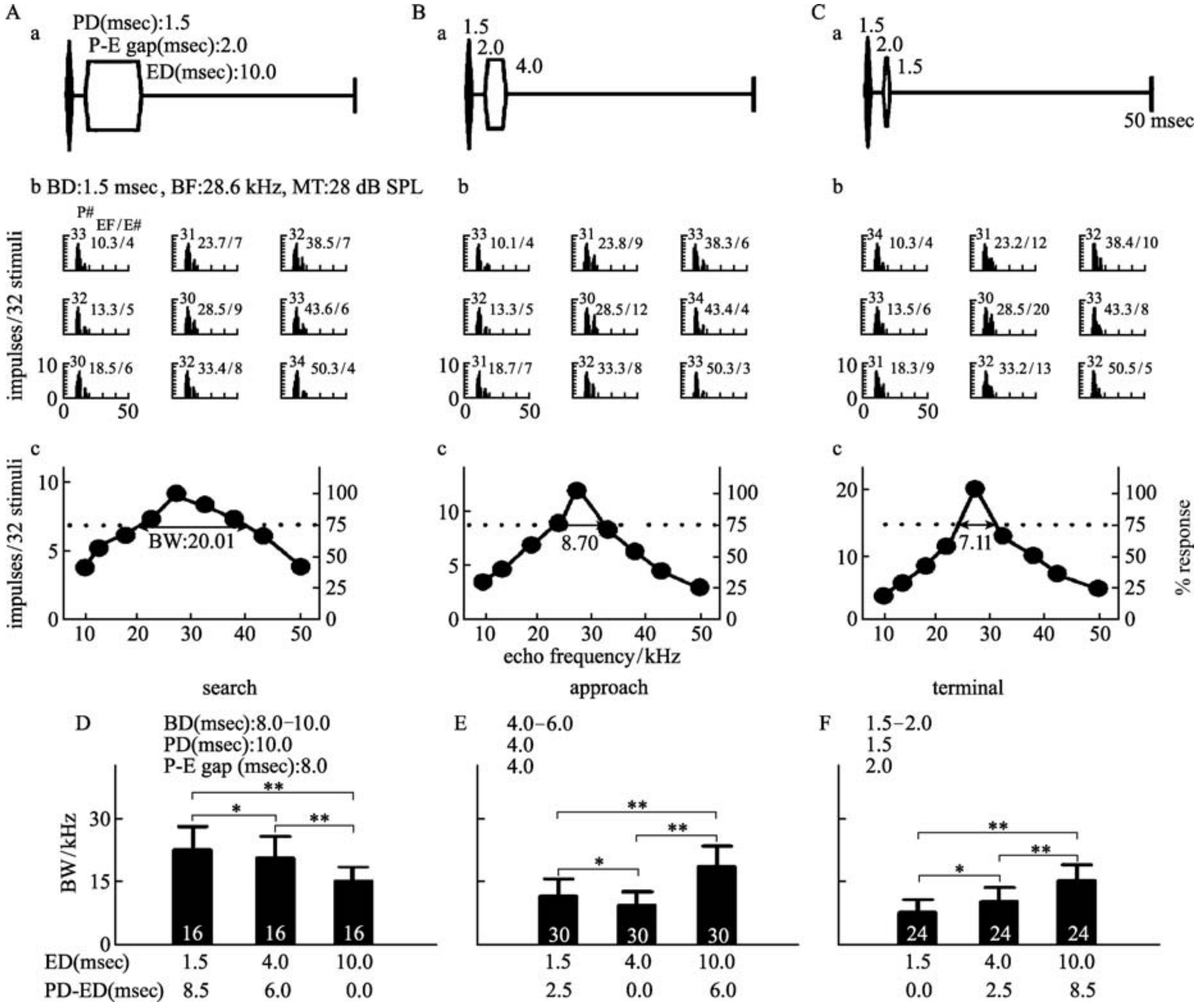

Fig. 16 Aa, Ba, Ca: Sketches of three P-E pairs used to study the echo iso-level frequency tuning curve (FTC) of collicular neurons of *Eptesicus fuscus*. The pulse duration (PD) was always 1.5 msec and the echo duration (ED) varied between 10, 4.0 and 1.5 msec. Ab, Bb, Cb: PST histograms showing the discharge pattern and the number of impulses of a colliculus neuron obtained with the 1.5 msec best frequency (BF) pulse (P#) and three echo durations (E#) at selected echo frequencies (EF). Respectively, the pulse and echo were delivered at 30 and 10 dB above the neuron's minimum threshold. Note that this neuron discharged the largest number of impulses to the BF echo pulses whose duration matched the neuron's BD (i.e. Cb, 28.5/20). Ac, Bc, Cc: The neuron's echo iso-level FTCs plotted with the number of impulses elicited by the echo pulse against the selected echo frequencies. Note that this neuron had the smallest bandwidth (BW) of 75% maximum when the echo iso-level FTC was plotted with 1.5 msec BD pulses (Cc). D, E, F: Bar histograms showing the average BW of the echo iso-level frequency tuning curve of colliculus neurons with three ranges of best duration determined with three P-E pairs at varied echo duration (ED). The echo duration and the difference between pulse and echo duration are shown below each bar. **: $P < 0.01$, *: $P < 0.05$ (From Wu and Jen, 2008).

complex sounds, this multiple-parametric corticofugal modulation can improve sub-cortical processing of these complex sounds.

In addition to improving ongoing subcortical signal processing, the corticofugal system also reorganizes subcortical auditory maps according to the acoustic experience in multiple-parametric domains (Sun et al., 1989, 1996; Yan and Suga, 1996; Jen et al., 1998, 2001, 2002, 2003; Jen and Zhou, 2003; Suga et al., 2000; Zhang and Suga, 2000; Zhang et al., 1997; Zhou and Jen, 2000a, b, c, 2005, 2007). This multiple-parametric corticofugal modulation can be independently mediated through the same subcortical neuron based on the difference in auditory selectivity between subcortical and cortical

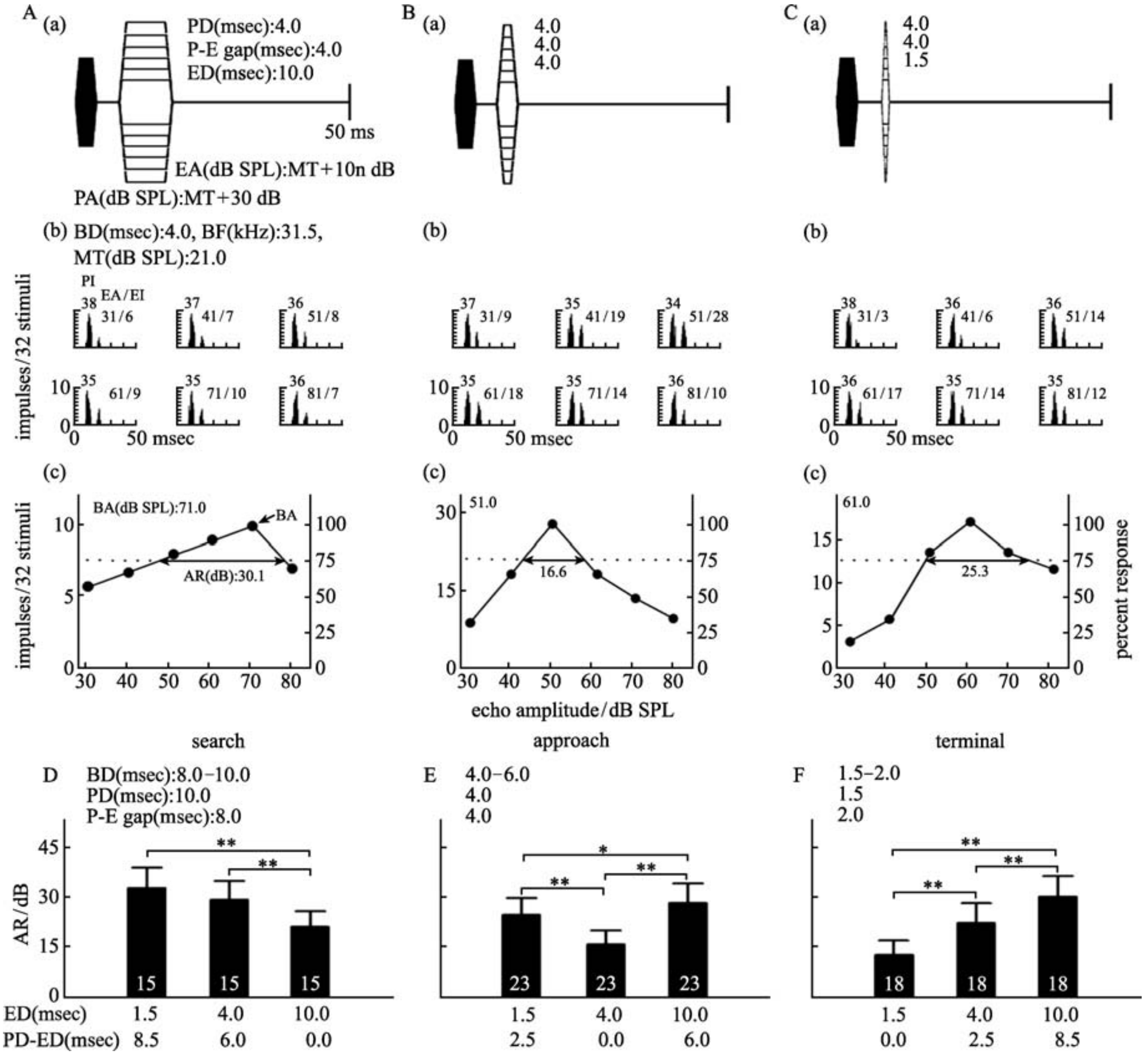

Fig. 17 Aa, Ba, Ca: Sketches of three P-E pairs used to study the echo rate-amplitude function (RAF) of collicular neurons. The PD was always 4.0 msec and the ED varied between 10, 4.0, and 1.5 msec at varied amplitudes. Ab, Bb, Cb: PST histograms showing the discharge pattern and the number of impulses of a collicular neuron obtained with 4.0 msec pulse (PI) at 10 dB above the MT and with three echo durations (EI) at selected echo amplitudes (EA). The neuron discharged the largest number of impulses to the BA echo pulses whose duration matched the neuron's BD (i.e. Bb, EA = 51; EI = 28). Ac, Bc, Cc: The neuron's echo RAF plotted with the number of impulses elicited by the echo pulse against the selected echo amplitudes. Note that this neuron had the smallest amplitude range (AR) of 75% maximum when the echo RAF was obtained with 4.0 msec BD pulses (Bc). D, E, F: Bar histograms showing the average AR of the echo RAF of collicular neurons with three ranges of BD determined with three P-E pairs at varied ED. The echo duration and the difference between pulse and echo duration are shown below each bar. **: $P < 0.01$, *: $P < 0.05$ (Wu and Jen, 2009).

neurons. As such, the corticofugally induced reorganization in each signal parameter is correlated with each signal parameter difference between subcortical and cortical neurons but not with differences in other parameters. Consequently, reorganization in a specific signal parameter would not be corticofugally induced when cortical and subcortical neurons have similar selectivity to a particular signal parameter (i.e. both cortical and subcortical neurons are "matched" in the selectivity to the same signal parameter) (Fig. 21).

In summary, the multiple-parametric corticofugal modulation of subcortical signal processing can actively improve signal-to-noise ratio for effective target detection and the analysis of target features by bats during hunting.

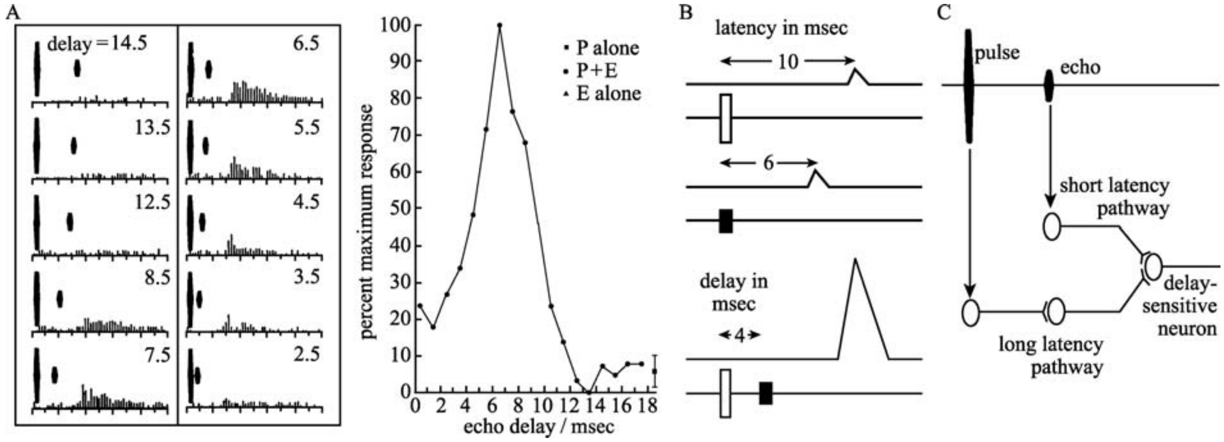

Fig. 18 A: The PST histograms showing the discharge pattern of a representative neuron of *Myotis lucifugus* in the medial geniculate body in response to a P–E pairs at varied P–E delays. The echo delay tuning curve shows a maximum at P–E delay of 6.5 msec. B: Sketches showing the discharge of a hypothetical delay tuning neuron in response to P, E and P–E pair. The neuron had a best delay of 4 msec. C: A sketch showing the neural circuits underlying the formation of delay–sensitive neuron. The P elicited response has a longer neural circuit than the E elicited response (From Sullivan, 1982b).

This multiple-parametric corticofugal modulation might also provide learned cognitive templates stored in memory from earlier experiences in echolocation.

2.10 A large area of the superior colliculus, pontine nuclei and cerebellum is sensitive to sound for sensori-motor integration

In auditory orientation, an animal listens to the sound and then orients itself toward the sound source. This auditory-guided behavior requires the animal first to detect and localize the sound before integrating and/or translating the processed auditory information to the motor areas (the premotor and primary motor cortex and supplementary motor area in particular). The motor areas then activate muscular activity via the descending motor control pathways to generate a specific pattern of head, pinna and/or body movement (Carpenter and Sutin, 1983; Martin, 1989). Thus, to ensure successful auditory orientation, the animal's auditory system should be sensitive to the spatial location of the sound source. Its brain should contain a center or centers which receive and integrate the spatial

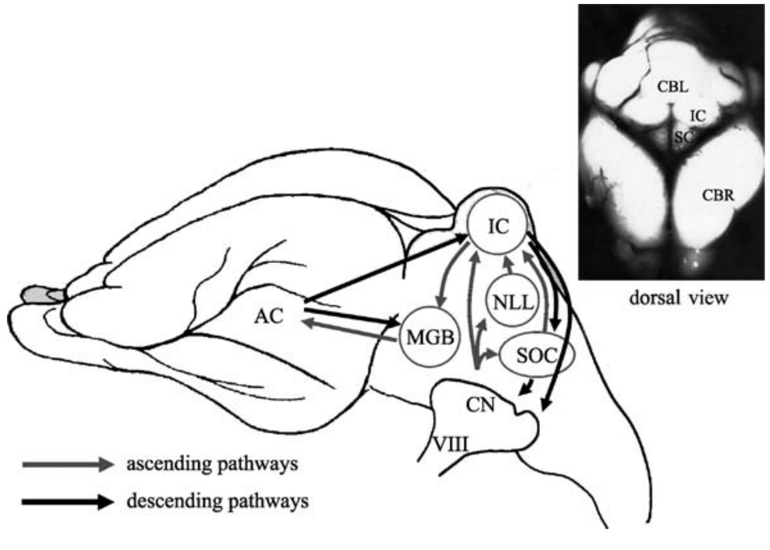

Fig. 19 A sketch showing the ascending and descending auditory pathways of a bat whose exposed brain in dorsal view is shown at the upper right. AC: auditory cortex; CBL: cerebellum; CBR: cerebrum; CN: coclear nucleus; IC: inferior colliculus; MGB: medial geniculate body; NLL: nucleus of the lateral lemniscus; SC: superior colliculus; SOC: superior olivary complex; VIII: the eighth cranial nerve.

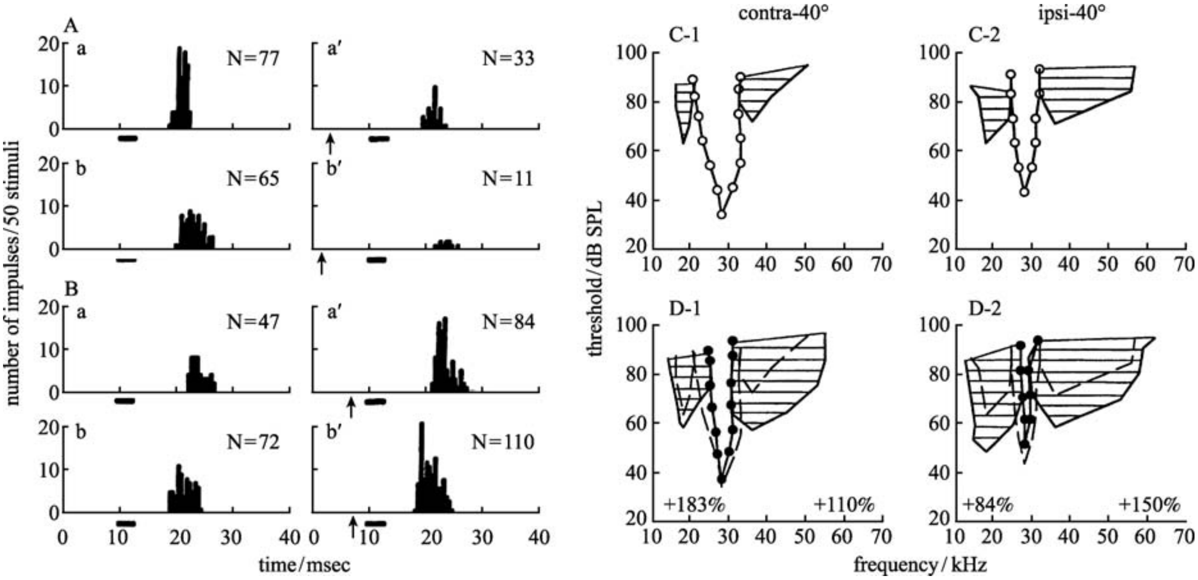

Fig. 20 PST histograms showing the inhibition (A) and facilitation (B) of responses of four collicular neurons of *Eptesicus fuscus* upon electrical stimulation in the auditory cortex (AC). Right and left columns show the responses of these neurons to best frequency sounds delivered at 10 dB above minimum threshold with and without cortical electrical stimulation. N: number of impulses in each PST histogram. Horizontal bar: acoustic stimulus. Arrows: cortical electrical stimulus. C, D: Excitatory (unfilled circles) and inhibitory (shaded area) threshold frequency tuning curves of a corticofugally inhibited collicular neuron obtained before (C-1, C-2) and during (D-1, D-2) cortical electrical stimulation at two sound directions. The inhibitory FTCs were plotted under two-tone stimulation conditions. For comparison, both excitatory and inhibitory FTCs are re-plotted (dashed line) in D-1 and D-2 (from Zhang et al., 2000).

information encoded by different levels of the auditory system and information from the motor cortex about the volitional movement executed or initiated before sending the spatial information to the cerebellum for further integration and fine-tuning of the orientation.

Anatomical studies have shown that auditory signals from the auditory cortex and the inferior colliculus terminate at the pontine nuclei which have reciprocal fiber connections with the cerebellum (Allan and Tsukahara, 1974; Kawamura, 1975; Mihailoff et al., 1981; Brodal, 1982; Cicirata et al., 1982; Wiesendanger and Wiesendanger, 1982a, b; Watt and Mihailoff, 1983; Azizi et al., 1985). The cerebellum is known to receive multisensory inputs and has been suggested to integrate incoming information from various neural pathways for regulation of motor responses to different sensory stimuli. The pontine nuclei also have reciprocal connections with the superior colliculus which receives its auditory inputs primarily from the inferior colliculus (Burne et al., 1981; Zhang et al., 1987). The superior colliculus (SC) of vertebrates is a multimodal integration center that is involved in orienting an animal's head, eyes and pinnae to novel stimuli (Sprague and Meikle, 1965; Wurtz and Goldberg, 1971; Stein et al., 1976; Harris, 1980).

Judging from the anatomical connections of the pontine nuclei to the higher auditory centers and to different brain areas involved in vocalization and motor orientation, the pontine nuclei may serve as centers of sensori-motor integration in auditory orientation. They may also serve as centers at which cerebellar outputs can be compared and reintegrated with auditory information and fed back to the cerebellum for follow-up motor correction.

Previous studies have shown that a large area of the superior colliculus, the pontine nuclei and the cerebellum of the bat, *Eptesicus fuscus*, contain neurons responding to sound stimulation (Jen and Schlegel, 1980; Jen et al., 1981, 1982, 1984a, b, 1993; Sun et al., 1983a, b, 1987; Shimozawa et al., 1984; Jen and Sun, 1988; Kamada and Jen, 1990; Kamada et al., 1992; Wu and Jen, 1995b, 1998; Figs. 22–24). These neurons are directionally sensitive such that they show maximal sensitivity to a sound delivered from a specific point within the frontal auditory space (the spatial response center) (Figs. 22 and 25). Furthermore, clear tonotopic organization as that shown in the inferior colliculus and auditory cortex is not evident in the superior colliculus, the pontine nuclei and the cerebellum (Jen et al., 1981, 1987, 1989; Sun et al., 1983b, 1987a; Shimozawa et al., 1984; Poon et al., 1990; Teng and Jen, 1990a, b; Kamada et al., 1992; Shen et al., 1997).

While the spatial response centers of neurons from the inferior colliculus (IC) and the auditory cortex (CBR) are

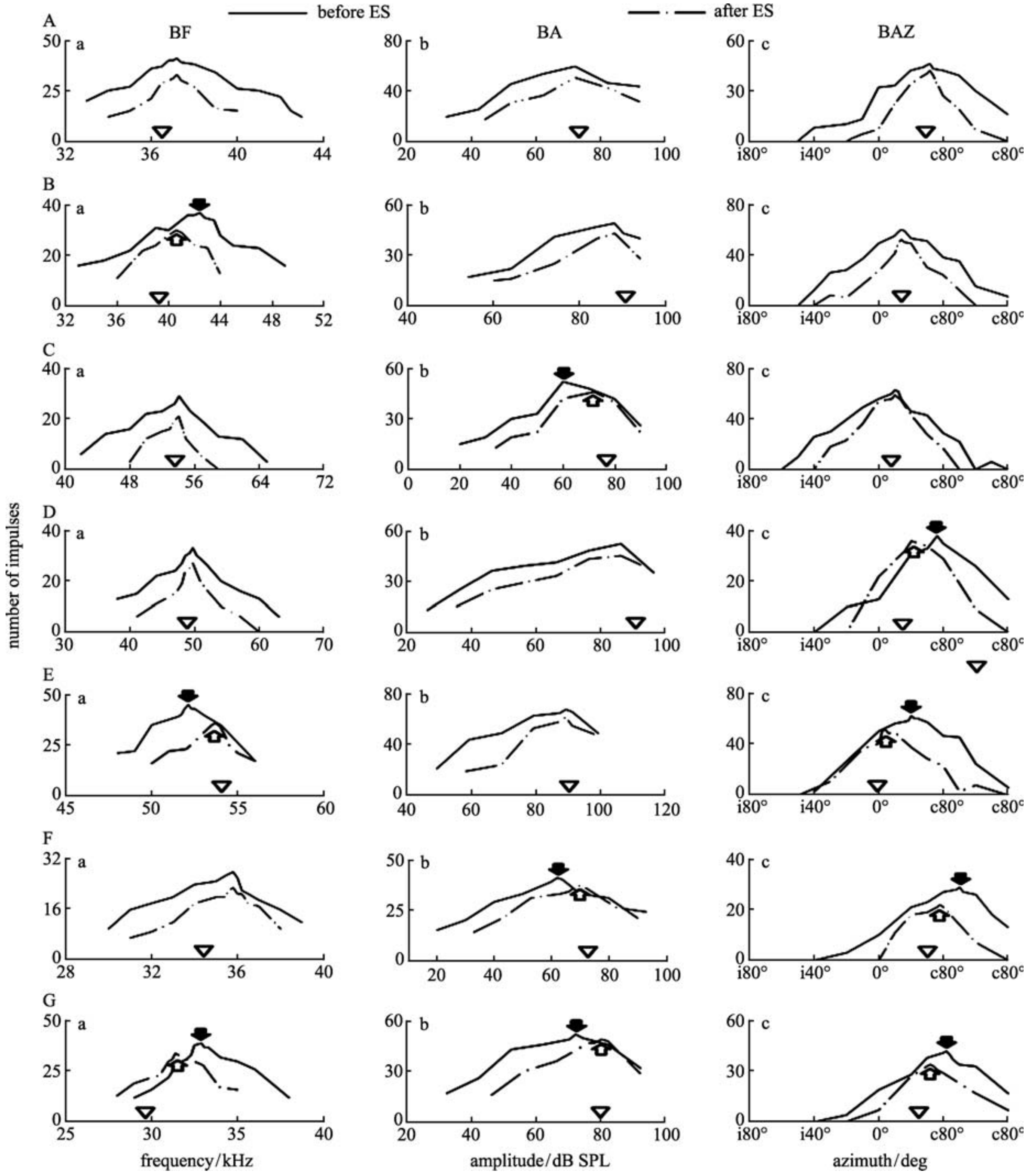

Fig. 21 Iso-amplitude frequency tuning curves, rate-amplitude functions, and directional tuning curves of 7 collicular neurons of *Eptesicus fusc*us plotted before (solid line) and after (dashed line) cortical electrical stimulation. The best frequency (BF), best amplitude (BA), and best azimuth (BAZ) of these neurons determined before and after cortical electrical stimulation are shown with filled and unfilled arrows while those of cortical neurons are shown with unfilled triangles. ES: cortical electrical stimulation. c or i, contralateral or ipsilateral to the recording site (Zhou and Jen, 2007).

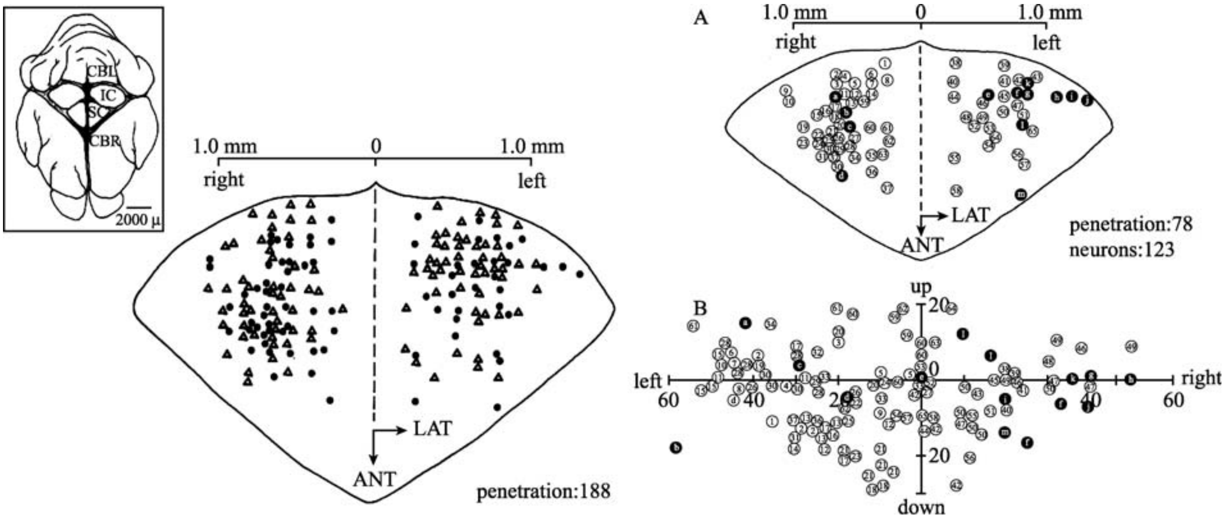

Fig. 22 Left: A composite map of superior colliculus (SC) of *Eptesicus fuscus* showing positions of 188 electrode penetrations. Those which did and did not record auditory units are shown in filled circles and unfilled triangles respectively. Inset: a sketch of the dorsal view of exposed brain showing the position of the SC relative to other parts of the brain. CBL: cerebellum; CRR: cerebrum; IC: inferior colliculus. Right: A: the locations of 78 electrode penetrations in the SC which isolated a total of 123 auditory neurons. B: the locations of spatial response centers of 123 units in the frontal auditory space of the bat. Circles with the same number or letter represent spatial response centers of auditory neurons which were isolated within the same electrode penetration. Note: neurons generally have their spatial response centers located at the contralateral portion or the frontal auditory space (Shimozawa et al., 1984).

mainly distributed in the bat's contralateral frontal auditory space, the spatial response centers of neurons from the superior colliculus (SC) and the pontine nuclei (PN) are located more closer to the midline or in the ipsilateral frontal auditory space (Fig. 25). Conversely, the spatial response centers of cerebellar auditory neurons are mostly located in the central portion of the bat's frontal auditory space. Thus, it appears that spatial response center begin to shift to the central frontal auditory space as auditory spatial information is transmitted from the auditory centers (IC and CBR) to the superior colliculus and the pontine nuclei. A further integration of spatial information apparently has taken place in the pontine nuclei before they send to the cerebellum resulting in a large number of cerebellar auditory neurons that are mostly sensitive to a frontal sound.

During hunting, a bat analyzes echoes and integrates all processed prey features to generate specific flight patterns and head orientation for prey capture. During the search phase, it uses its rather narrowly beaming sonar signals to scan its environment in order to locate targets (Shimozawa et al., 1974; Schnitzler and Grinnell, 1977). Once a target of interest is located, the bat's head would seem to be always pointing at the target (Webster and Brazier, 1965; Masters et al., 1985). Judging from the forward beaming of its sonar signals and the funneling characteristics of its forward-oriented pinnae, a bat certainly would bring its localized prey within its frontal gaze during the final phase of pursuit.

As the cerebellum is known to receive multisensory input (Snider and Stowell, 1944; Fadiga and Pupilli, 1964) and at the same time is considered to be a part of the extrapyramidal motor system, it is reasonable to believe that the cerebellum uses sensory information to regulate motor responses. Conceivably, the cerebellum of a bat should be able to utilize the spatial information and to coordinate with the motor cortex in order to orient the head toward a localized echo source. The fact that most spatial response centers of cerebellar auditory neurons are located within a small area of the central portion of the frontal auditory space suggests that the cerebellum is able to orient the bat's head toward the localized target within its frontal gaze. It has been demonstrated that the majority of the cerebellar auditory neurons in cats are also most sensitive to a frontal sound (Aitkin and Rawson, 1983).

3 Conclusions

This article reviews behavior and electrophysiological studies underlying the bat biosonar behavior. Adaptive mechanisms underlying a bat's successful hunting include: (1) Forward orienting and highly mobile pinnae for effective scanning, signal reception, sound pressure transformation and mobile auditory sensitivity; (2) Avoiding and detecting moving targets more successfully than stationary ones; (3) Coordinated activity of highly developed laryngeal and middle ear muscles during pulse emission and reception; (4) Mechanical and neural attenuation of intense emitted pulses to prepare for better reception of weak returning echoes; (5) Increasing pulse repetition rate to improve multiple-parametric selectivity to

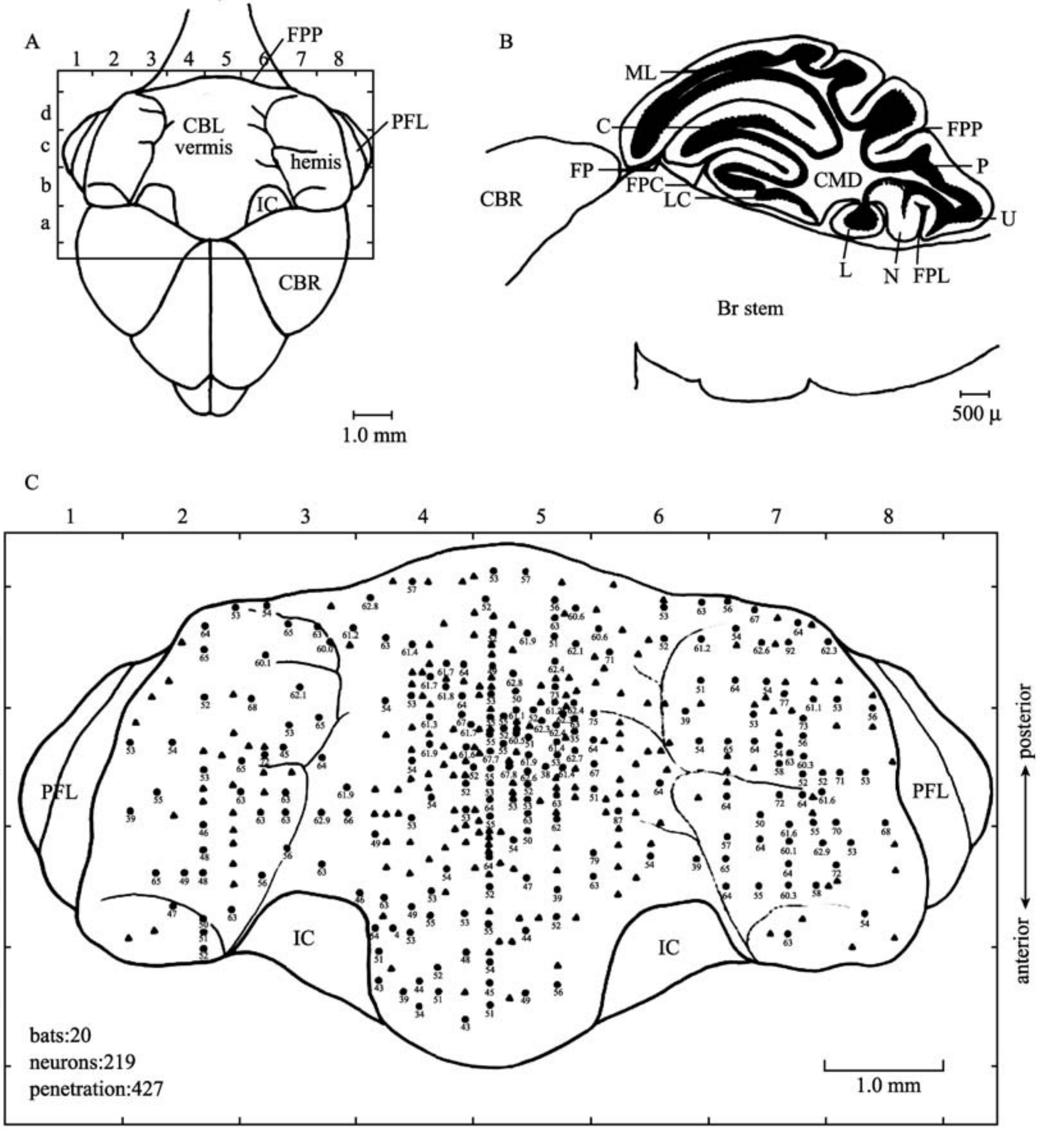

Fig. 23 A, B: a sketch of the dorsal and mid-sagital view of the brain of the CF-FM bat, *Pteronotus parnellii parnellii.* Br stem: brainstem; C: culmen; CBL: cerebellum; CBR: cerebrum: CMD: cerebellar medulla; FP: fissura prima; FPC: fissure preculminata; FPL: fissura posterolateralis; FPP: fissura prepyramidalis; hemis: hemisphere; Ie: inferior colliculus; L: lingulacerebelli; LC: lobulus centralis; ML: lobus medium of Ingvar; N: nodulus; P: pyramis vermis; PFL: parallocculus; V: uvula vermis. C: a composite map of the auditory representation on the exposed cerebellum (rectangle in A). A total of 427 electrode penetrations were performed on the cerebella of 20 bats in which 219 penetrations encountered neurons responding to sound stimulation (Sun et al., 1983a, b).

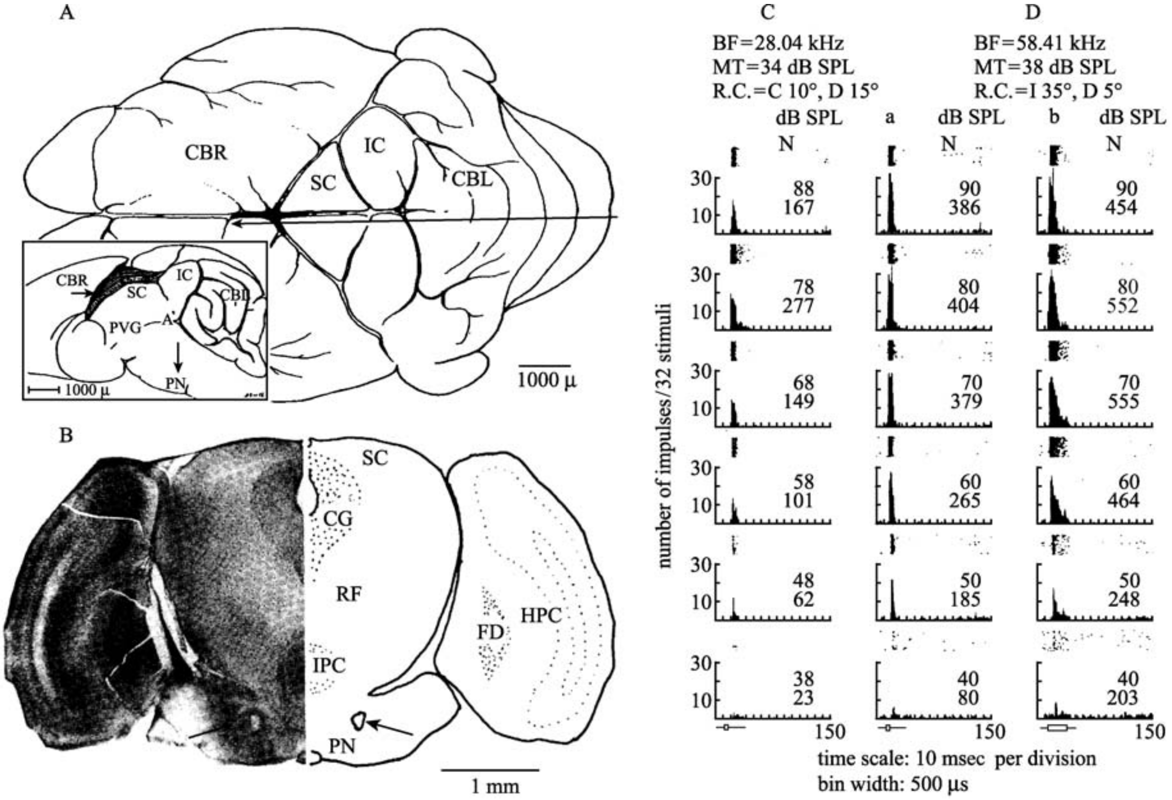

Fig. 24 A: a sketch showing the dorsal view and sagittal view of a bat's brain. B: a coronal section through the midbrain of *Eptesicus fuscus* showing a lesion site (arrow) inside the pontine nuclei. CG: central gray; FD: fascia dentata; HPC: hippocampus; IPC: interpeduncular nucleus; PN: pontine nuclei; RF: reticular formation; SC: superior colliculus. C, D: PST histograms and dot-raster patterns of a phasic burster (C) and a tonic responding pontine neuron (D). The tonic neuron discharged impulses throughout the whole duration of the stimulus, thus its number of impulses increased greatly when the stimulus duration was increased from 4 to 25 msec (Da *vs* Db). I: ipsilateral portion of the frontal auditory space (From Kamada et al., 1992).

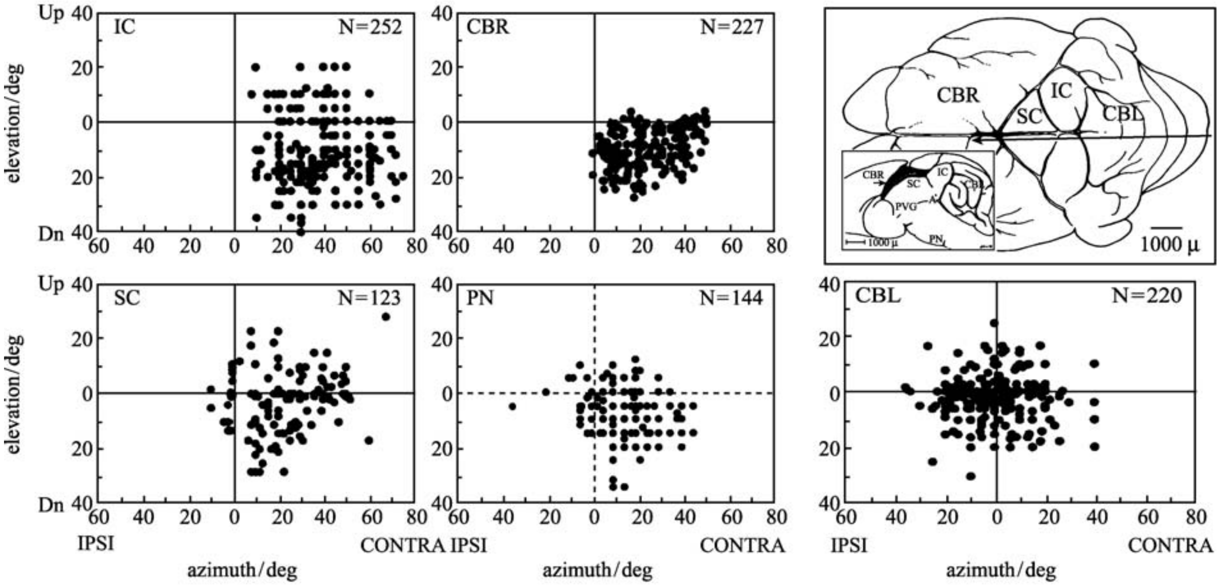

Fig. 25 The distribution of spatial response centers of neurons isolated from the inferior colliculus (IC), auditory cortex (CBR), superior colliculus (SC), pontine nuclei (PN) and cerebellum (CBL) of *Eptesicus fuscus*. N: the number of neurons in each distribution. The two solid lines represent the horizontal and vertical planes crossing the center point of the bat's frontal auditory space (Kamada et al., 1992).

echoes; (6) Dynamic variation of duration selectivity and recovery cycle of auditory neurons with hunting phase for better echo analysis; (7) Maximal multiple-parametric selectivity to expected echoes returning within a time window after pulse emission; (8) Pulse-echo delay-sensitive neurons in higher auditory centers for echo ranging; (9) Corticofugal modulation to improve on-going multiple-parametric signal processing and reorganize signal representation, and (10) A large area of the superior colliculus, pontine nuclei and cerebellum that is sensitive to sound for sensori-motor integration. All these adaptive mechanisms facilitate the bat to effectively extract prey features for successful hunting.

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