Neurophysiological Analysis of Echolocation in Bats

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IN THE EARLY 1940's, Griffin and Galambos placed an array of fine wires from the ceiling to the floor of a flight room and studied the echolocating behavior of bats flying across the array. When the bats come close to the array of wires, they increase the rate of sound emission and cross the array. Little brown bats (*Myotis lucifugus*) dodge wires as thin as 0.2 mm (refs. 1 to 3). What part of the brain carries out the most essential processing of the acoustic information necessary for echolocation?

EFFECTS OF ABLATION OF THE INFERIOR COLLICULUS OR AUDITORY CORTEX ON OBSTACLE AVOIDANCE

Cat cortical auditory areas are essential for sound localization. When their auditory cortices are bilaterally ablated, cats lose the ability to localize a sound source (refs. 4 and 5). Since unilateral ablation, however, has little effect on sound localization, the importance of the cortical auditory areas does not depend on information processing—through the corpus callosum—based on interaction between both of the hemispheres (ref. 6).

Transection of the corpus callosum and/or the commissure of the inferior colliculus does not affect the ability to localize a sound source (ref. 7). In cats, the most essential cue for accurate sound localization is produced as a result of binaural interaction in the superior olivary nuclei and is utilized only in the presence of the cortical auditory areas.

What part of the bat's brain is the highest center for echolocation? The lower levels of the bat's auditory system, including both the cochlear nucleus and the inferior colliculus, are enormously hypertrophied; but this is not true of either the medial geniculate body or the auditory cortex (ref. 8). Bilateral ablation of the auditory cortex has almost no effect on echolocation across the array of wires (ref. 9). The bat's auditory cortex seems to be less important for sound localization than that of the cat.

Bilateral ablation of the inferior colliculus reduces the ability to echolocate. The effect depends on the extent of the inferior collicular lesion. Figures 1 to 3 illustrate three examples of echolocation after inferior collicular ablation. In figure 1, the dorsal part of the inferior colliculus is bilaterally ablated. The ability to dodge even 0.2-mm wires is

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Legend:
X------X —copper wires of 0.2-mm diameter

Δ------Δ —0.5-mm copper wires

●------● —1.9-mm polyethylene tubings
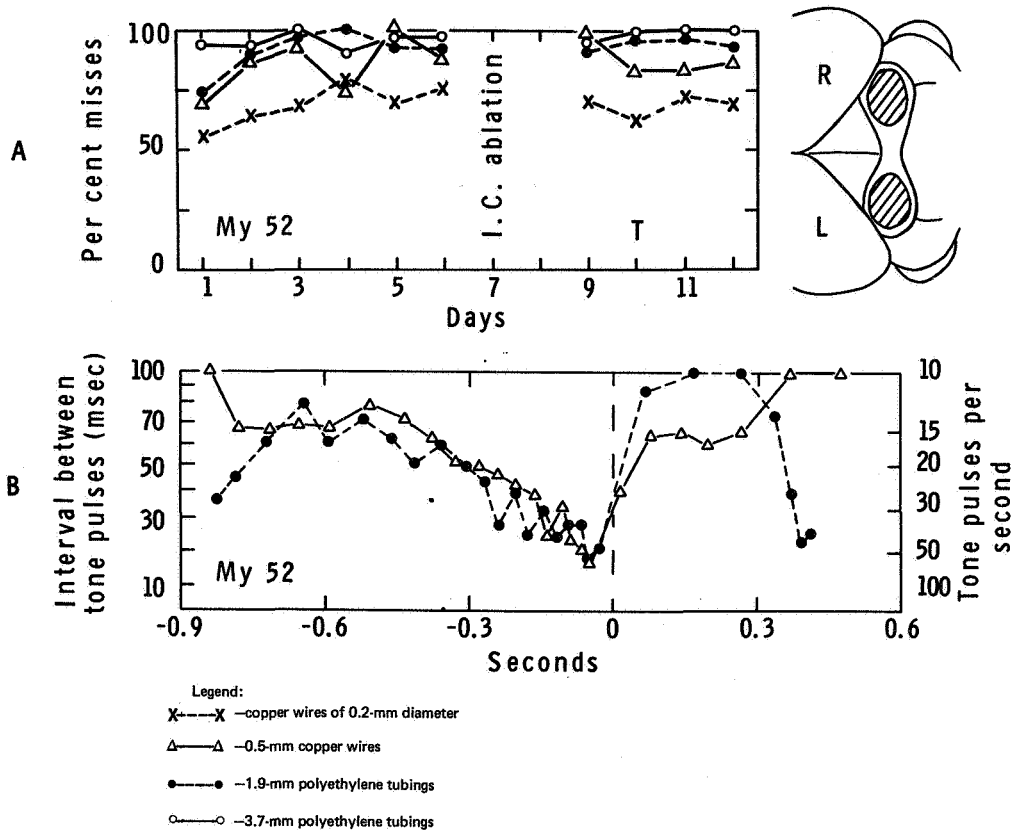
O------O —3.7-mm polyethylene tubings

FIGURE 1. Ability to avoid obstacles before and after ablation of the dorsal part of I.C. (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 52 (*Myotis yumanensis*). In A, ordinate and abscissa represent percent of misses of strands and days since the task of obstacle avoidance was first given to the bat. To the right, dorsal view of mid-brain region is sketched. Shaded areas indicate ablation of I.C. In B, the ordinate represents interval between orientation sounds emitted by the bat in msec to the left and rate of sound emission in tone pulses/sec to the right. Abscissa shows time before and after crossing obstacles in sec. Repetition rate of sound emission increases up to higher than 50/sec immediately before crossing the obstacles. T in A indicates a day on which data presented in B were obtained (ref. 10).

not affected at all, and the change in the rate of sound emission is also normal. Echolocating ability is impaired, however, when the bilateral ablation extends to the ventral part and includes a part of the main nucleus (fig. 2). In this figure the bat always increases the rate of sound emission for wires larger than 0.5 mm at least 0.3 to 0.6 sec before crossing

them, although it cannot dodge the 0.5-mm wires. This result indicates that the bat notices the presence of the fine wires, but the analysis of echoes is insufficient in spite of the emission of many orientation sounds.

Very severe unilateral ablation of the inferior colliculus, including a part of the lateral lemniscus, has almost no effect on the
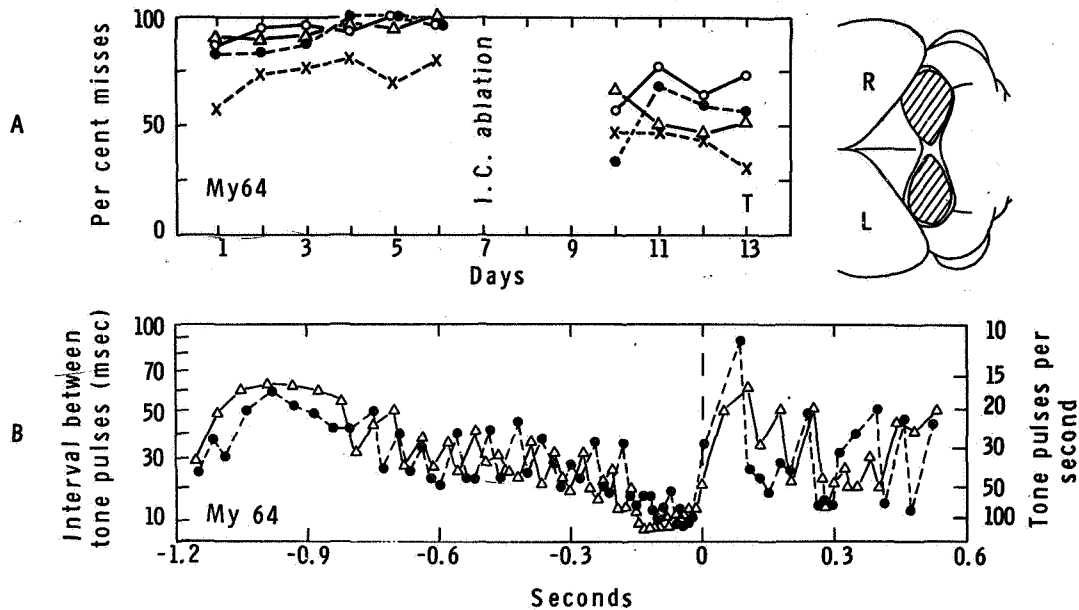
FIGURE 2. Obstacle-avoidance performance before and after I.C. ablation including a part of the main nucleus (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 64 (*Myotis yumanensis*). Note decrease in percentage of misses (A) and emission of many orientation sounds preceding obstacle avoidance after bilateral ablation of I.C. (B). All symbols have same meaning as in figure 1 (ref. 10).

ability to avoid obstacles (fig. 3). The animal can dodge even 0.2-mm wires. When both of the colliculi are severely ablated, the bat starts to emit orientation sounds at an unusually high rate; but it is unable to avoid even the 3.7-mm polyethelene tubing. The bat shows no signs of obstacle detection and even crashes into the wall (fig. 3). From a series of similar experiments, it has become clear that the main nucleus of one of the inferior colliculi is necessary for processing information essential for echolocation (ref. 10). It is not necessary to compare the activity in the right and left lateral lemnisci or higher auditory nuclei for sound localization.

Information necessary for echolocation is supplied to the inferior colliculus from the superior olivary and cochlear nuclei through the lateral lemniscus. At least two questions about echolocation must thus be considered: what kind of information the inferior colliculus receives from the lower levels of the auditory nuclei and how the information is processed in the inferior colliculus. Neurophysiological data that have been obtained can be reviewed from different aspects such as echo-detection, echo-ranging, echo-localization, and echo-analysis. The following sections are mainly a review of some of the data about echo-detection and echo-ranging.

ECHO-DETECTION AND ELECTRICAL ACTIVITY OF AUDITORY NEURONS IN THE MID-BRAIN

The relationship between ablation, obstacle avoidance, and evoked potential changes
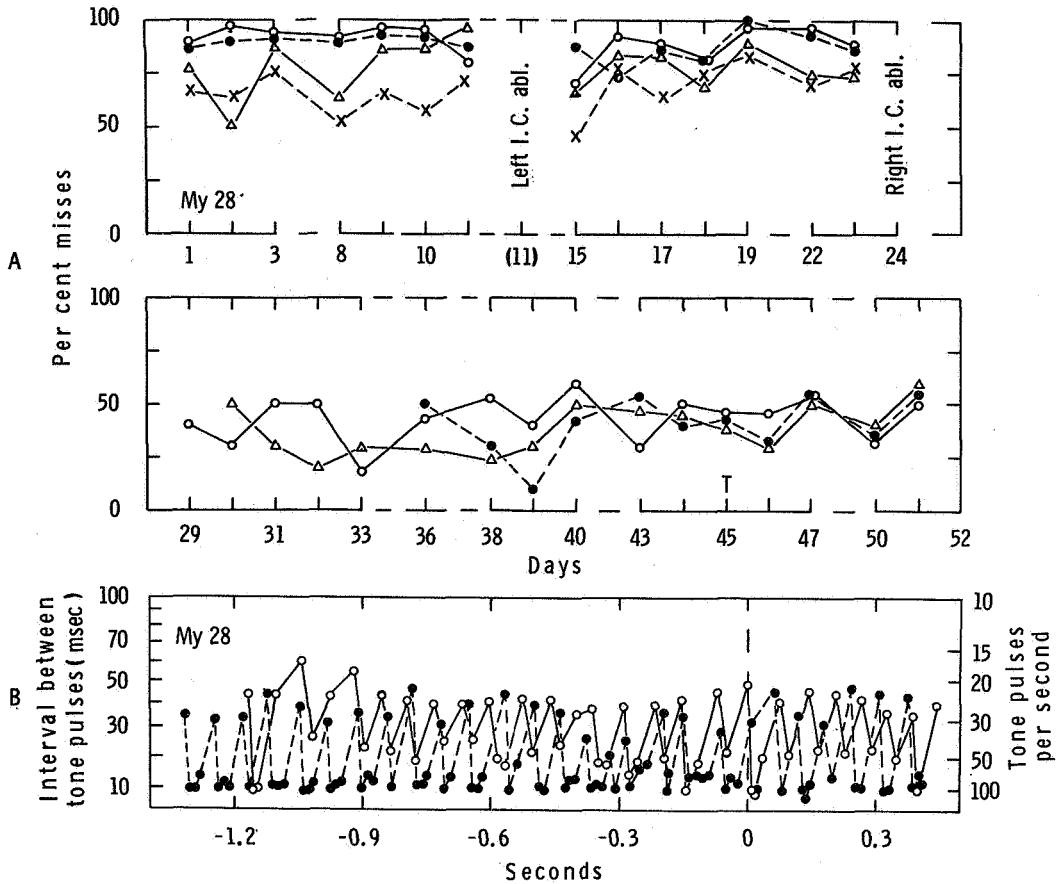
FIGURE 3. Obstacle-avoidance performance before and after severe I.C. ablation (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 28 (*Myotis yumanensis*). Since severe unilateral ablation of I.C. has no effect on ability to avoid obstacles (upper graph in A), the other I.C. is also ablated severely. Then the bat cannot avoid even the 3.7-mm strands (lower graph in A) in spite of frequent emission of orientation sounds (B). All symbols have same meaning as in figure 1 (ref. 10).

is schematically expressed in figure 4. When a recording electrode is placed on the dorsal surface of the inferior colliculus, two distinct positive potential changes evoked by a sound stimulus of 30 to 50 kHz are recorded. The fast component has a peak latency of about 3 msec, and the slow component has a peak latency of 7 to 9 msec (fig. 4B). Since the bat's brain is small, the summated activity of the auditory nerve and medullary auditory nuclei are often simultaneously recorded as shown in figure 4B. The fast component, called N_4 (ref. 11), mainly represents the summated activity of ascending lateral lemniscal fibers and the slow component represents that of the inferior collicular neurons. The shape and amplitude of these evoked potential changes vary with the frequency and amplitude of the sound stimulus and the location of the recording electrode, because
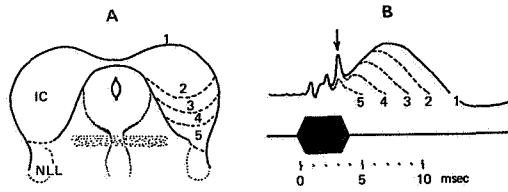
C. Effect of bilateral ablation of I.C. on echo-location

(1) Avoids even strands of 0.2 mm diameter.
(2) The same as above.
(3) Hits fine strands, but avoids coarse ones.
(4) Hits even strands of 3.7 mm diameter.
(5) The same as above.

FIGURE 4. Schematic presentation of the relation between I.C. ablation (A) and evoked potentials (B). Evoked potentials shown by B1 are recorded with a recording electrode placed on the dorsal surface of I.C. (A1). Certain components of the evoked potentials are, however, affected (B, 2 to 5) by successive ablation of the I.C. from the dorsal side (A, 2 to 5). In B, acoustic delay of the stimulus is corrected. Arrow indicates activity of ascending lateral lemniscal fibers. In C, ability to avoid obstacles after bilateral ablation of I.C. is described. In C, 1 to 5 correspond with 1 to 5 in A and B (ref. 10).

of the tonotopic organization of the inferior colliculus and incoming lateral lemniscal fibers (refs. 10, 12 and 13).

Interestingly the lateral lemniscal (L.L.) evoked potential shows a short recovery cycle and follows repetitive stimuli at a high rate. In other words, the information about echoes coming back from a distance as short as 8 cm is sent into the inferior colliculus. The auditory nervous sytem appears to show adaptation for echo-detection (ref. 14). This adaptation of the auditory system appears to be established between 7 and 10 days after birth. On the fifth day after birth, most of the middle ear cavity is still filled with mesenchyme. The cochlear nerve fiber sends information about repetitive stimuli to the brain at a high rate, but the L.L. fibers cannot convey this information to the inferior colliculus. The L.L. evoked potential shows a long latency—6

msec instead of 3 msec (fig. 5).[1] The nerve fibers in the brain are probably not yet myelinated at this time.

Unlike the L.L. evoked potential, the inferior collicular (I.C.) evoked potential shows a long recovery cycle. The properties of these evoked potentials are very different (ref. 12). This indicates that extensive information processing takes place in the inferior colliculus. In fact, unlike the cochlear nucleus, the inferior colliculus contains various types of neurons. Some of these are specialized for responding to an echo coming back from a certain distance or direction or for responding to an echo with a certain amplitude and structure. According to Grinnel[1] (ref. 14), some collicular neurons recover very quickly and sometimes show a supernormal phase in their recovery cycles. These neurons appear to be specialized for echo-detection.

EFFECT OF CONTRACTION OF MIDDLE EAR MUSCLES ON ECHO-DETECTION

For echo-detection, bats have not only the particular neural mechanism described above, but also a muscular mechanism. The middle ear muscles start to contract 4 to 10 msec earlier than sound emission and relax within 10 msec after the emission. The maximum contraction occurs at the moment of sound emission and reduces the stimulation of the bat's own ear as much as 20 dB (ref. 15). In cats, the middle ear muscles also contract preceding and during vocalization (ref. 16), but it is not as precisely timed as in bats.

The contraction of the middle ear muscles of bats actually improves detection, especially for echoes coming back from distances of more than 1 m. Figure 6A shows the re-

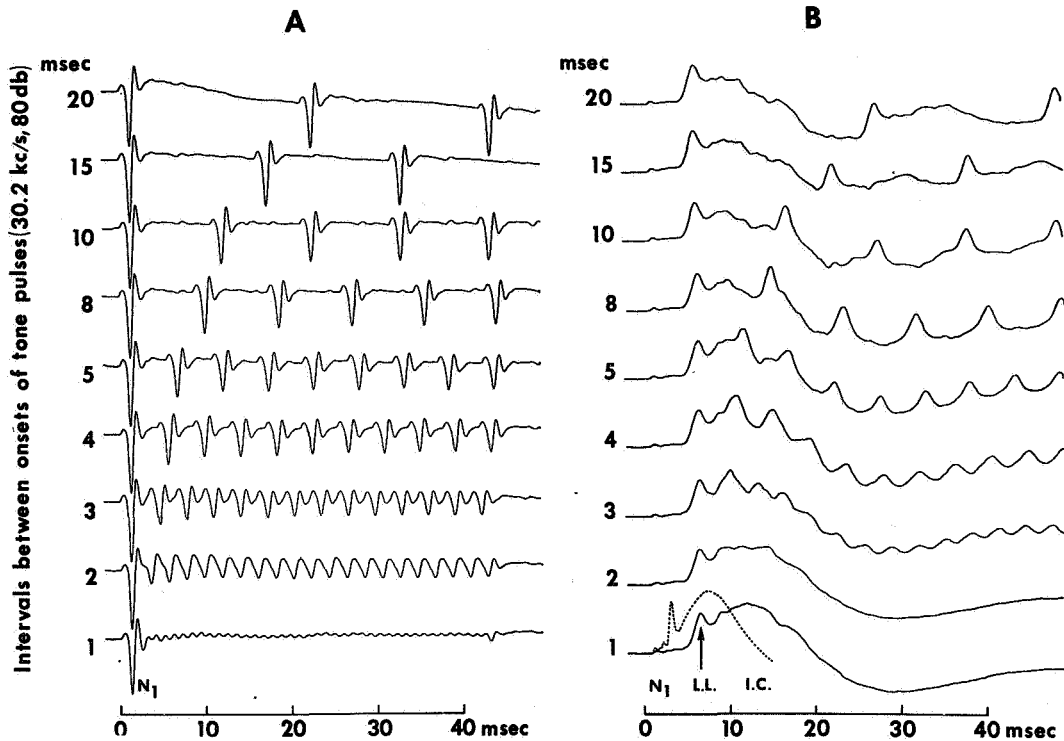[1] Data by N. Suga and D. Crawley, unpublished.

FIGURE 5. Responses to trains of 30.2 kHz, 80-dB SPL tone pulses, recorded from round window (A) and dorsal surface of inferior colliculus (B) of a 5-day old bat (*Myotis lucifugus*). Duration and rise time of each tone pulse were 0.5 msec and abrupt, respectively. Tone pulse was delivered intermittently during a 40-msec period which is indicated by time scale at bottom. Intervals between onsets of pulses is indicated to left of each trace. This train of pulses was delivered at a rate of two per sec. Responses to 64 trains were averaged with a computer, as shown in each trace. A—N_1 response. B—L.L. (arrow) and I.C. evoked potentials. N_1 follows repetitive stimuli at 1000 pulses per second. L.L. evoked potential fails to follow stimuli at about 400 pulses per sec. I.C. evoked potential does not follow stimuli at 80 to 90 pulses per sec. Note long latency of L.L. evoked potential. Shape of the I.C. evoked potential at the bottom of B is same as that evoked by 40-msec tone burst. Dotted curve shows L.L. and I.C. evoked potentials recorded from an adult bat (Suga and Crawley, unpublished data).

covery cycles of the I.C. evoked potential. When the first tone pulse is attenuated from 90 dB to 70 dB, for example, the recovery cycle of the response to the second tone pulse of 80 or 60 dB shortens. Since the evoked potential is a mass response, this shortening in recovery cycle may be considered to be the average change of many single neurons. The change in the recovery cycles of some collicu-

lar neurons is much more prominent than that in the recovery cycle of the I.C. evoked potential (fig. 6B and 6C).

INFERIOR COLLICULAR NEURONS SPECIALIZED FOR ECHO-RANGING

A basic clue for measurement of the distance to an object is given by the time lag

between the outgoing orientation sound and the returning echo. This time lag is presumably coded in the time difference between the responses of a neuron to the outgoing sound and the echo. Three questions must thus be asked:

(1) How is the zero time point reset?

(2) How is the arrival time accurately detected?

(3) How is the time lag measured?

The latency of response of a neuron to a stimulus generally changes as a function of stimulus amplitude and rise time. If the amplitude of a stimulus such as an outgoing sound is very large and quickly increases beyond the threshold of a neuron, the latency of response of the neuron will be short. If the amplitude of a stimulus such as an echo is just above the threshold of the neuron or if it slowly increases up to the threshold, the latency of response will be long. When this occurs, a large error will be introduced into distance measurement. Therefore, for echo-ranging there must be neurons that show relatively constant latency regardless of stimulus amplitude and rise time. If such neurons discharge multiple impulses in response to a single stimulus, there will be no way to distinguish between one strong echo and a few weak echoes. There must, therefore, be "latency-constant neurons" that do not fire repetitively for a single stimulus. Furthermore, the neurons must be spontaneously inactive. Any neurons satisfying the above requirements may be considered to be specialized for the measurement of distance and may be called "echo-ranging neurons."

Unlike the cochlear nuclear neurons, most neurons in the inferior colliculus show no spontaneous discharges and fire only a few impulses at the onset of a sound stimulus (ref. 17). Most of the phasic on-responding neurons are not latency-constant units. The latency of response changes to a great extent
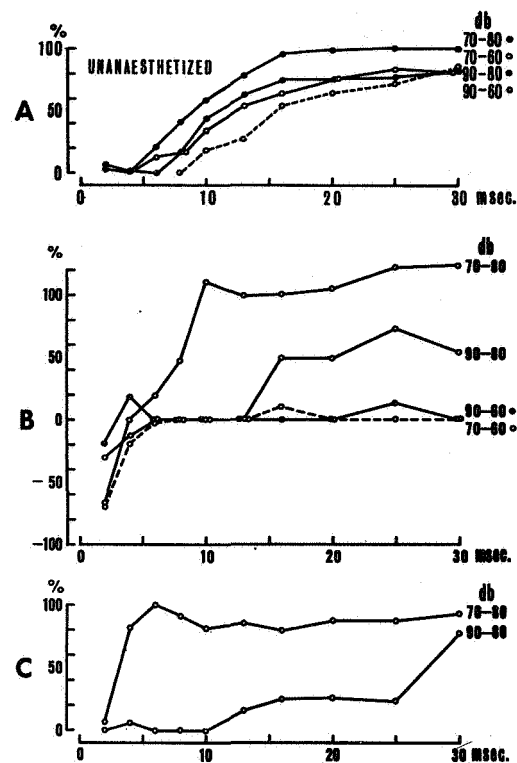

FIGURE 6. A—averaged recovery cycles of I.C. evoked potential obtained from five unanesthetized bats (*Myotis lucifugus*). B and C—recovery cycles of two inferior collicular neurons of anesthetized bats (*M. lucifugus*). Abscissas represent interval between onsets of a pair of FM tone pulses. Ordinates represent response to second tone pulse in percentage. Over 100 percent response signifies that the second pulse produced as large an evoked potential (A) or as many impulses (B and C) as when delivered alone; O means only the response to the first pulse, and negative values mean that even the response to the first pulse was reduced by percentage indicated. Amplitude of a pair of FM tone pulses is shown to the right of each curve (e.g., 70 to 80 means first tone pulse was 70-dB SPL, and the second, 80-dB SPL). Note changes in recovery cycle with change in relative amplitudes of tone pulses (ref. 12).
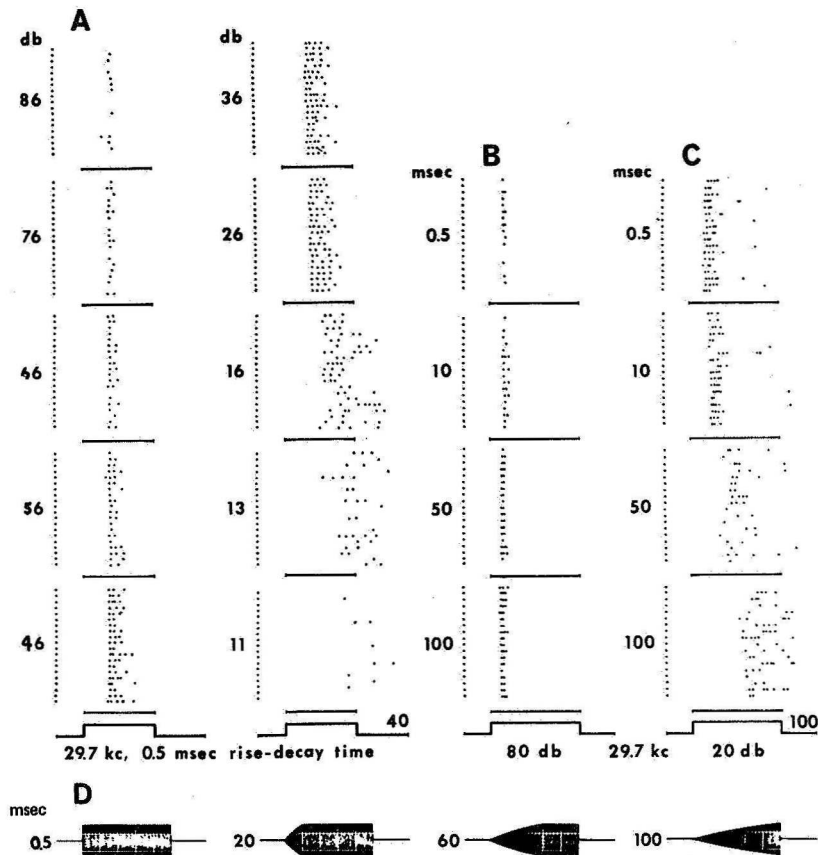
FIGURE 7. Responses of an inferior collicular neuron which was not specialized for echo-ranging (*Myotis lucifugus*). Responses to repeated presentations of same tone pulse are shown by a dotted pattern in which one dot corresponds to the peak of one action potential. Sweep of a cathode-ray oscilloscope was displaced vertically before each stimulus. Dots to the left mark the start of the sweep. Sound stimulus is represented by a horizontal bar and square wave at bottom of each dotted pattern. In A, the amplitude of a 29.7-kHz tone burst with a 0.5-msec rise-decay time and a 40-msec duration was attenuated from 86- to 11-dB SPL. In B and C, the rise time of a 29.7-kHz tone burst with a 100-msec duration was changed, as indicated by number to left of each dotted pattern. Decay time was always 0.5 msec. Peak amplitude of tone burst was 80-dB SPL in B and 20-dB SPL in C. Note changes in latency of response and number of impulses. In D, four samples of the 100-msec tone bursts used are shown (ref. 31).

with stimulus amplitude and rise time (fig. 7). Some of the phasic on-responding neurons, however, have the properties of the echo-ranging unit (ref. 31). For example, the neuron in figure 8 discharges one or less than one impulse per stimulus regardless of stimu-

lus frequency, amplitude, and rise time. The latency of response stays almost the same regardless of stimulus amplitude. At 96 dB, the latency of the response to a tone burst with a 0.5-msec rise time was 5.7 ± 0.27 msec. Even if the amplitude was attenuated down to 56
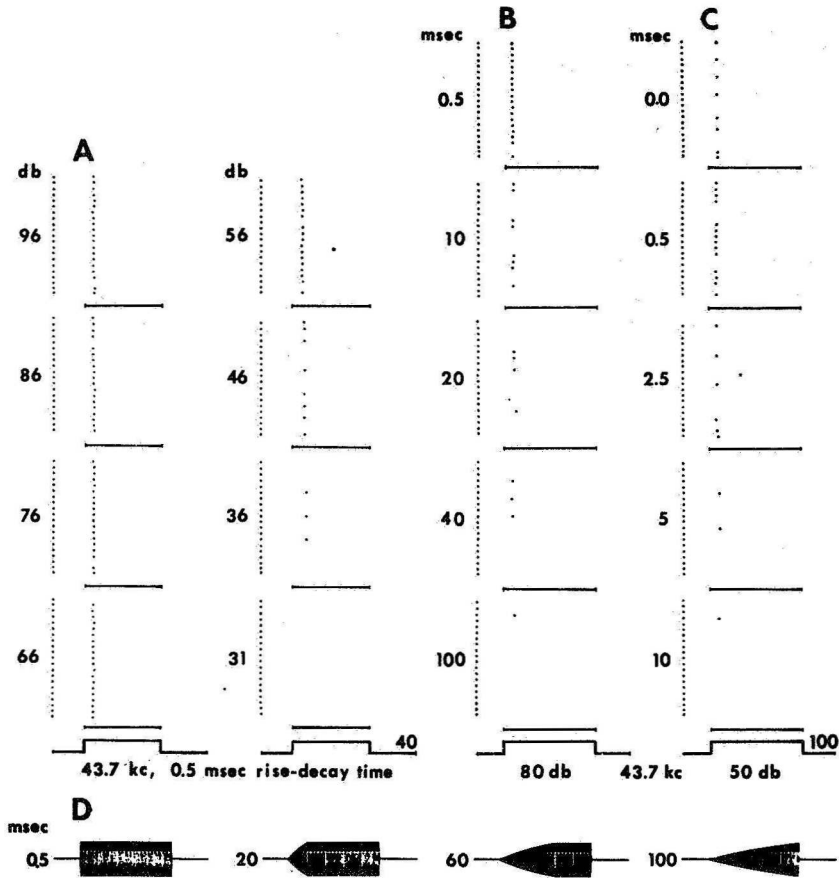
FIGURE 8. Responses of echo-ranging neuron in inferior colliculus (*Myotis lucifugus*). In A, the amplitude of 43.7-kHz tone burst with 0.5-msec rise-decay time and 40-msec duration is attenuated from 96- to 31-dB SPL. In B and C, rise time of a 43.7-kHz tone burst with 100-msec duration was changed, as indicated by number to left of each dotted pattern; decay time was always 0.5 msec. Peak amplitude of tone burst was 80-dB SPL in B and 50-dB SPL in C. Note that the number of impulses is always one or less than one, and the response latency does not fluctuate more than ±1.0 msec even if probability of response decreased down to 0.5. Symbols have the same meaning as in figure 7 (ref. 31).

dB (one one-hundredth), the latency was 6.2 ± 0.20 msec. Both the latency of response and the number of impulses per stimulus changed only a little, so the neuron can hardly code stimulus amplitude in this range. At the threshold amplitude the number of impulses per stimulus is very small. When an impulse does appear, however, its latency is nearly constant (fig. 8A). When the rise time of a tone burst increases from 0.5 to 98 msec, the number of impulses per stimulus becomes very small. When the response does appear, however, its latency stays within a very limited range (fig. 8B).

The minimum slope of the amplitude increase necessary for excitation of the neuron

is obtained by plotting the threshold of the response against the rise time (fig. 9). In figure 9, the threshold-rise time curves, a and b, make contact at 4 to 5 msec with the straight dashed lines which indicate the minimum slope. This means that the neuron can respond only to a tone burst with an amplitude which reaches the threshold within 4 to 5 msec, and that the "critical latency shift" due to the rise time is 4 to 5 msec. The smallest critical latency shift obtained was 1 msec. Since only a tone burst that quickly increases in amplitude can excite the neuron, the change in latency due to an increase in rise time is very limited in these neurons. The properties of these echo-ranging neurons can be explained by accommodation or a simple neural network model involving an inhibitory neuron.

We now know that the inferior colliculus receives impulses that are well synchronized with shortly spaced tone pulses, and that

some of the inferior collicular neurons are specialized for the accurate detection of the onset of a stimulus. We should furthermore determine how the bat measures the time lag of an echo from the orientation sound. For the measurement of a time lag, the auditory system must include some kind of clock that is reset by each outgoing orientation sound. After being excited by the orientation sound, auditory neurons become insensitive for a certain period of time. The recovery cycle of response is more or less similar in all single units studied in the auditory nerve and cochlear nucleus (ref. 18). In the inferior colliculus, however, the duration of the recovery cycle varies considerably from neuron to neuron (fig. 10). Some neurons recover very rapidly, while others recover very slowly. This spectrum of recovery times may provide a mechanism for scaling the time lag of echoes returning from objects at different distances (ref. 12).
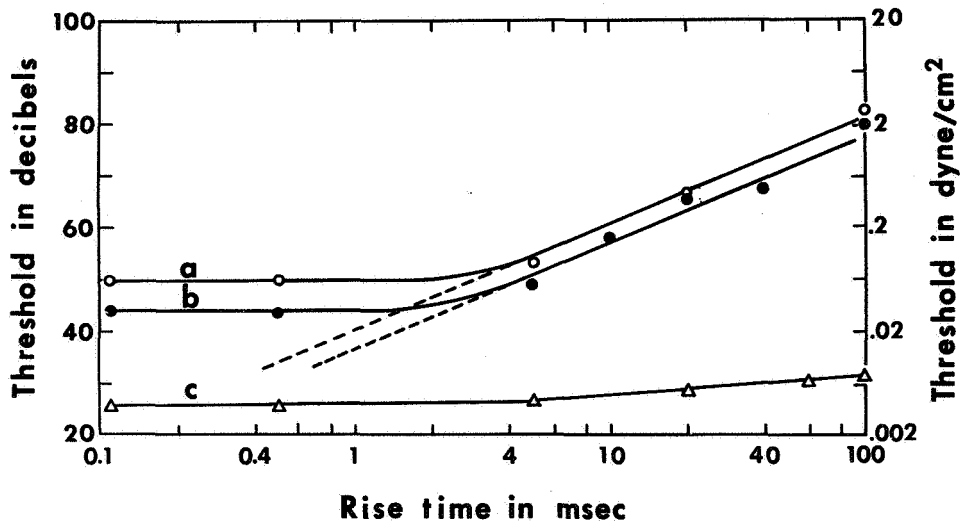

FIGURE 9. Change in threshold of response of three neurons (a, b, and c) with rise time of tone burst set at best frequency (*Myotis lucifugus*). Duration and decay time of the tone burst were 100 and 0.5 msec, respectively. Frequency of the tone burst was 70-kHz for a, 32-kHz for b, and 50-kHz for c. Dashed lines indicate minimum slopes of stimuli which excited neurons a and b (ref. 31).
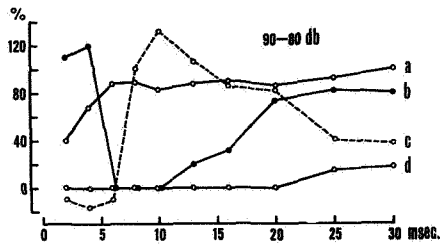
FIGURE 10. Four types of recovery cycles in the inferior colliculus (*Myotis lucifugus*). (a) short suppression, (b) delayed inhibition, (c) temporary recovery, and (d) undelayed inhibition. These were measured in four single neurons with a pair of 4-msec FM tone pulses, the first, 90-dB SPL and the second, 80-dB SPL. Ordinate represents response; abscissa, represents interval between onsets of first and second tone pulses in msec. A 100-percent response corresponds to number of impulses per second tone pulse when it was delivered alone. In these examples, this value was 1.00 for a, 2.75 for b, 1.28 for c, and 1.58 for d (ref. 12).

SOME NEUROPHYSIOLOGICAL DATA CONCERNING ECHO-LOCALIZATION

The structure of the superior olivary complex of bats, where binaural interaction first takes place, differs from that of cats (ref. 19). In cats, some of the neurons in a superior olivary complex are sensitive to very small interaural time and intensity differences (refs. 20 and 21). The properties of these neurons fit a neural model for sound localization (ref. 22). In the cat's inferior colliculus, there are neurons further specialized for processing information about sound localization. These neurons are very sensitive to either interaural time (or phase) or intensity differences (ref. 23). No comparable investigations have been performed on bats as yet.

The interaural intensity and phase differences due to the shadowing effect of the head and pinnae vary with stimulus frequency, so that the waveform of a complex sound at each ear is quite different from that of the

original complex sound (refs. 24 and 25). The complex sound is more easily localized than is a pure tone. Pumphrey (ref. 26) explained how an animal could localize a sound source by listening to only a few short complex sounds delivered from it. His theory states that sound localization is accomplished by the binaural comparison of intensity ratios at three different frequencies to which the ears show different polar diagrams. To test this, measurements have been made of the polar diagrams of the ears of owls and bats, and it has been demonstrated that these polar diagrams change extensively with the frequency of sound and also with the position of the external ear (refs. 13, 27 and 28).

SOME NEUROPHYSIOLOGICAL DATA CONCERNING ECHO-ANALYSIS

Some insectivorous bats emit tone pulses that are variously modulated in amplitude and frequency. Echoes coming back from objects at different places overlap each other and show complex envelopes and structures differing from those of the outgoing sounds. In the inferior colliculus of these bats, there are neurons that are specialized for the analysis of a particular type of sound (refs. 29 and 30). One of the most interesting types of neurons is the FM-specialized neuron which responds to FM sounds but not to pure tones and noise bursts. For excitation of such a neuron, the direction, range, speed, and functional form of frequency sweep are important factors. Two factors which determine whether or not a complex sound will excite this type of neuron are the presence of a particular FM component within the sound and the components which exist simultaneously with the FM component. The nature of the sound preceding the complex sound is also an important factor.

Since most collicular neurons show phasic

on-responses to tone bursts, the rising phase of stimulus amplitude is very important for their excitation. Some neurons are sensitive to a fast rate of amplitude increase, while others are sensitive to a slow rate of increase. The shape and size of the tuning curves of some collicular neurons change greatly with the rise time of the sound used for the measurement (ref. 32). Some collicular neurons are specialized for responding only to sounds with a small amplitude (ref. 11). Some collicular neurons thus appear to have the capacity to analyze not only the frequency structure of echoes but also their amplitudes. In other words, these neurons can analyze echoes carrying information concerning such things as the size and surface properties of a target.

ACKNOWLEDGMENT

DISCUSSION

QUESTION: Have you calculated sensitivity spectrums according to different frequencies?

SUGA: The frequency sensitivity of neurons differs from neuron to neuron. Some neurons are sensitive to 30 kc, while others are sensitive to 60 kc. There are a variety of neurons, each of which is tuned for a particular frequency of sound.

KLEEREKOPER: Do you assume that the mechanism you described serves as a timer?

SUGA: Yes, it is possible.

GRIFFIN: Have you compared the stability, the constancy of latency, with Dr. James Simmons' data on distance discrimination?

SUGA: The latency of response to a tone burst always shows some fluctuation, which introduces an error in echo-ranging. Responses of single neurons so far studied appear to be insufficient for explaining the fine distance discrimination demonstrated in the behavioral experiments because the standard deviation of a latency histogram is not very small. Further experiments on echo-ranging neurons and the statistical treatment of responses to artificial outgoing sounds and echoes should be performed. A neuron with interesting response properties was found in the inferior colliculus. That is, the latency of response to the second tone pulse showed a standard deviation much smaller than that of the latency of the response to the first one. There may be some neural mechanism by which the fluctuation in the latency of response is reduced.

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