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FUNCTIONAL PROPERTIES OF AUDITORY NEURONES IN THE CORTEX OF ECHO-LOCATING BATS

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The auditory cortex has been considered to be the highest centre of processing auditory information. After complete bilateral ablation of cortical areas, cats are able to make discriminations of frequency (Butler, Diamond & Neff, 1957; Neff & Diamond, 1958; Goldberg, Diamond & Neff, 1958; Rose & Woolsey, 1958) and also of intensity (Raab & Ades, 1946; Rosenzweig, 1946), but not of temporal pattern of tones (Diamond & Neff, 1957; Goldberg, Diamond & Neff, 1957). The discharge pattern of single neurones in the auditory cortex of cats is a phasic 'on' response to tone stimuli (Erulkar, Rose & Davies, 1956; Hind, 1960). The response areas (areas above frequency response curves, Galambos & Davis, 1943) of such neurones are wider than those in the medial geniculate body, although the neural networks from the cochlear nucleus to the geniculate body generally tend to produce narrower response areas (Katsuki, Watanabe & Maruyama, 1959).

In echo-locating bats, the auditory system from the cochlear nucleus to the inferior colliculus is enormously hypertrophied compared to most other mammals, but this is not true of either the geniculate body or the auditory cortex (Poljak, 1926; Zvorykin, 1959). Thus the inferior colliculus seems to be the highest centre specialized by anatomical hypertrophy for echo-location. Single unit activity in the inferior colliculus shows that the discharge pattern is a phasic 'on' response caused by excitatory and inhibitory interplay. The response areas of some neurones are narrower, but others are wider than in the cochlear nucleus (Suga, 1964*a*, 1965). The responses of inferior collicular units with narrow response areas to frequency modulated (FM) tone pulses are variously modified by inhibitory areas located on one or both sides of the response areas. On the contrary, units with wide response areas are not sensitive to frequency change of sounds (Suga, 1965). If neurones with wide response areas exist dominantly in the auditory cortex of bats as in cats, the auditory cortex of the bat

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may be less differentiated to analyse the minor differences among echoes than the colliculus, or cortical neurones may be differentiated in some ways other than those in the colliculus.

The auditory cortex of the bat has not previously been studied electrophysiologically. This paper describes neural activity recorded from the cortex, and compares such activity with that found in the inferior colliculus. The auditory cortex was first located by evoked potentials. Then single units were studied on stimulation with pure and FM tone pulses.

METHODS

Thirty-three bats, *Myotis lucifugus*, anaesthetized with the intraperitoneal injection of 45 mg/kg Nembutal (pentobarbital sodium) were used for the experiments. Ether was used at the initial phases of operation if necessary to stop movement of animals. The experiments were conducted for 6–7 hr without an additional injection of Nembutal, in an electrically shielded room at 35–37° C. The cerebral cortex is visible through the thin skull after removal of the temporal muscles. In order to study the evoked potential, a large hole (3–7 mm^2) was made in the skull and the dura mater was torn. Then a 3 M-KCl glass pipette micro-electrode with a tip diameter of nearly 1 μ (15–25 MΩ) was put on the cortical surface. For single unit recording a hole as small as possible (0·2–0·3 mm^2) was made in the skull with sharpened forceps and the dura mater was torn. When the hole was small enough, the movement of the cortex due to respiration and blood pressure was so small that a closed system for recording was not always necessary (Davies, 1956; Hubel, 1959). A glass pipette microelectrode filled with 3 M-KCl solution (30–60 MΩ) was inserted into the cortex perpendicularly through the small hole by a hydraulic micromanipulator. During penetration a 4 msec pure tone pulse and a 4 msec FM tone pulse were delivered alternately. When impulses were recorded, discharge patterns, response (excitatory) and inhibitory areas, responses to FM tone pulses, spike-count functions and recovery cycles were studied.

Recording and stimulating equipment was the same as that employed in previous experiments (Suga, 1964*a*, *b*, 1965). The pure and FM tone pulses with 4 msec durations and 0·5 msec rise-fall times in intensity were delivered from two similar loudspeakers calibrated with a Bruel and Kjaer Model 4153 condenser microphone. The maximum output of the two loudspeakers used are shown by the uppermost curves in Figs. 9 and 10. All sound intensities in this paper are expressed in db re 0·0002 dyne/cm^2 peak-to-peak. These absolute values are accurate within ± 2 db. The intensity within the FM tone pulse was not uniform but varied with frequency even at a constant input voltage. The intensity of the FM tone pulse was therefore expressed as attenuation below the maximum intensity available from the loudspeaker, i.e. by the vertical position of the arrow parallel to the maximum output curve. The range of the frequency sweep of each FM tone pulse and its direction, rising or falling frequency, are shown by the horizontal position of the arrow and its head (see Fig. 3).

RESULTS

Evoked potentials from the auditory cortex

The cortex of *Myotis lucifugus* has no gyri. Blood vessels on the surface of the brain show much variety in their patterns and it is even difficult to find any homologue of the sylvian or ectosylvian gyrus of the cat. A composite, typical pattern of blood vessels was obtained from thirty brains (Fig. 1*A*). A square area (5·1 mm^2) which included the whole auditory area determined by evoked potential study was located on the temporal

region of the cerebrum (Fig. 1*A*). This area was arbitrarily divided into nine equal divisions for convenience of description (Fig. 1*B*).

When a glass pipette micro-electrode with a low resistance (15–25 MΩ) was placed on the cerebral surface within the square, a positive-negative

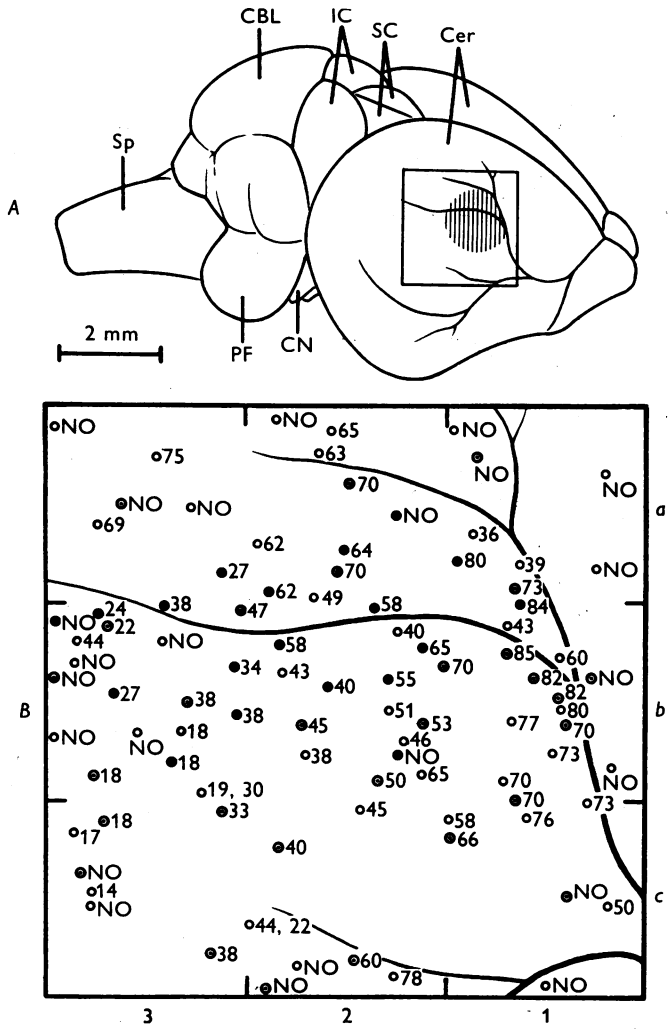


Fig. 1. *A*. Diagram of bat's brain. Surface positive-negative evoked potentials were recorded in most places within the square (see *B*). Single unit activity was mainly recorded from the shaded area where the evoked potential was most prominent. CBL: cerebellum, Cer: Cerebrum, CN: cochlear nucleus, IC: inferior colliculus, PF: parafloccullus, SC: superior colliculus, Sp: spinal cord. *B*. Tonotopic localization within the square in *A* as studied in three bats. The figures represent the best frequencies (kc) of evoked potentials at that point. The three experiments with different bats are recorded by open circles, filled circles and circles with dots at centre. NO indicates a place where no evoked potential was recorded.

diphasic potential change evoked by a pure tone pulse was recorded (Fig. 2*A*, 1). The positive phase began to rise with a 7–8 msec latency and reached a peak 11–12 msec after the onset of stimulus. In animals which showed prominent evoked potentials the auditory area covered most of the square.

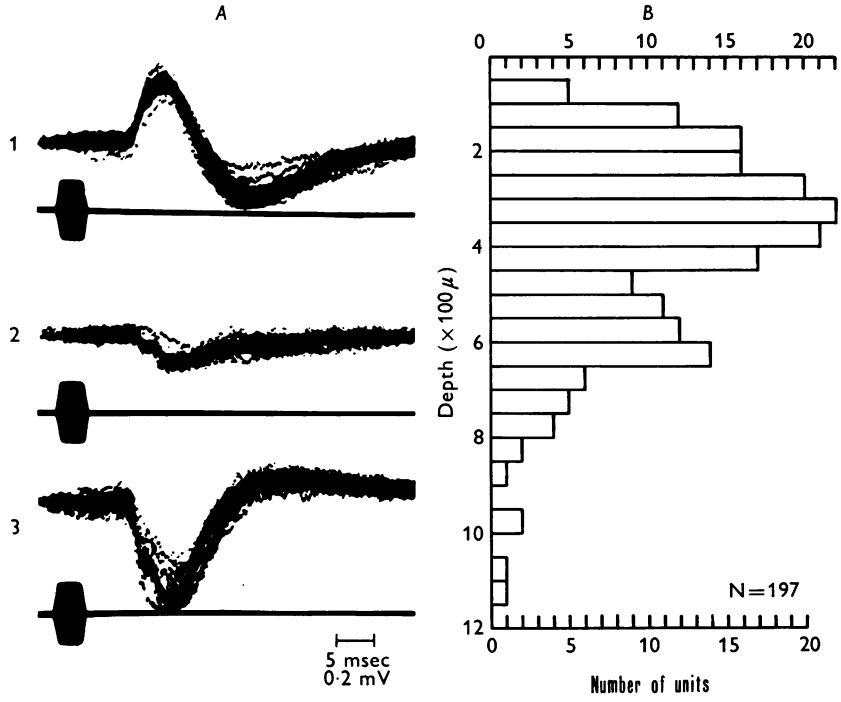


Fig. 2. *A*. Potential changes evoked by a 71·3 kc, 107 db tone pulse as recorded, (1) at the cortical surface, (2) at a depth of 150 μ and, (3) at a depth of 300 μ. Twenty traces were superimposed in each photograph. Positive deflexion is upward. The length of the short horizontal scale represents 5 msec and also 0·2 mV vertically. Acoustic delay in air (1·8 msec) is not corrected.

B. Distribution of depths below the cortical surface where 197 single units were recorded.

The evoked potential was most prominent at the posterior half of the division 1*b*, while it was so faint near the anterior edge of area 1 that this region was probably not included in the auditory area (Fig. 1*B*). In animals which showed poor evoked potentials, they were recorded in a small region indicated by the shaded area in Fig. 1*A*. In other words, the evoked potential was always recorded in this region which presumably corresponded to the primary auditory cortex in cats (Ades, 1943; Rose, 1949; Woolsey, 1961).

Since a well localized evoked potential change could be recorded with a micro-electrode of low resistance, tonotopic localization in the auditory

cortex was studied by moving the electrode to various places on the cortical surface. The distribution of best frequencies for evoked potentials studied in three bats is shown in Fig. 1*B*. The bat's audiogram has its minimum threshold at 35–40 kc (Grinnell, 1963). In zone '*a*' of Fig. 1*B*, a group of neurones sensitive to frequencies higher than 60 kc was dominantly localized but there was no gradient in best frequency. However, a clear frequency gradient was found in zone '*b*' where high frequency neurones were localized anteriorly and low frequency ones posteriorly. In division 1*b*, the threshold curve of evoked potential sometimes showed double peaks in sensitivity, the first peak (minimum threshold) at 70–85 kc and the second at 15–30 kc. The difference in threshold between them was 30–50 db. The single-unit study described below seemed to show that this evoked potential was not caused by intermixture of units some sensitive to high and some to low frequency, but by units with response areas showing two minima (Fig. 5*A*). Evoked potentials with the minimum threshold ranging between 15 and 30 kc were also recorded in division 3*b*. The minimum threshold was, however, 30–50 db lower than the second minimum for the evoked potential which was sensitive to 15–30 kc in division 1*b*. In zone '*c*', the evoked potential was recordable, but its amplitude was relatively smaller than in zone '*b*'. Thus single-unit activity was mainly studied within the shaded area including 1*b* and 2*b* (Fig. 1*A*).

When the micro-electrode was inserted into the auditory cortex, the positive-negative evoked potential at the surface gradually decreased in amplitude. By further advancement of the electrode, the polarity of the evoked potential changed into negative-positive diphasic (Fig. 2*A*, 3). The depth at which the polarity change occurred ranged from 70 and 150 μ, being deeper near a large blood vessel. The amplitude of the negative-positive evoked potential was maximum between 150 and 450 μ. Sometimes the positive phase was so faint that the evoked potential seemed to be negative monophasic. A transverse section of the auditory cortex shows that near a large blood vessel the cell layer begins at the depth of about 150 μ from the exposed cortical surface, and at about 70 μ elsewhere. The polarity of the evoked potential seemed to change when the tip of the electrode was in the cell layers (Katsuki, Watanabe & Maruyama, 1959).

Discharge patterns of single units

Single unit activity was scarcely ever encountered when the evoked potential was positive-negative diphasic, but it was recorded when the evoked potential became minimum and changed its polarity. The depth of the tip of the micro-electrode was simply read off a scale after contact noise between the electrode and the cerebrum had appeared. The distribution of 197 single units isolated at various depths (Fig. 2*B*) indicated that

these neurones were mainly recorded from the cell layers under the superficial plexiform layer. Latencies of these units ranged from 8 to 22 msec, but most were between 11 and 17 msec. Cortical cells seemed to show more phasic 'on' responses and longer recovery cycles than those in the inferior colliculus (Suga, 1964*b*). Spontaneously active units were rare. 'Off' responses were not found when pure tone pulses 4 or 40 msec long were used. However, it has been found that in cortical neurones the discharge pattern becomes more phasic and recovery cycle is lengthened by anaesthesia (Derbyshire, Rempel, Forbes & Lambert, 1936; Jarcho, 1949; Erulkar *et al.* 1956; Katsuki, Murata, Suga & Takenaka, 1959; Kiang, Neame & Clark, 1961; Schoolman & Evarts, 1959) as is also true in other parts of the brain (Heinbecker & Bartley, 1940; Poggio & Mountcastle, 1963).

The relation between sound intensity and number of impulses (it is called the spike-count function by Rose, Greenwood, Goldberg & Hind, 1963) was non-monotonic in 63% of forty units studied. That is, the number of impulses first increased with the intensity of sound stimulus and then decreased with further strengthening of the stimulus. In 22%, number of impulses was monotonically increased with the increasing intensity. In the remaining 15%, the spike-count was nearly independent of intensity over a wide range from 50 to 100 db. When present, spontaneous activity or injury discharges were commonly inhibited by sound stimuli. But three neurones displayed spontaneous discharges that were not inhibited by tonal stimuli, while responses to them showed long recovery cycles.

Best frequencies and minimum thresholds of neurones recorded within single punctures

Single units recorded within each puncture seemed to have similar best frequencies. Figure 3 shows response areas for pure tone pulses and thresholds for FM tone pulses which were measured in three different punctures

Legend to Fig. 3

Fig. 3. *A*, *B*, and *C* show response areas for pure tone pulses and thresholds to FM tone pulses of single neurones recorded in three single punctures. Scales of sound intensity (db re 0·0002 dyne/cm^2 peak-to-peak) and depths at which the neurones were found are given on the left and right sides of each response area (open circles) respectively. The range of the frequency sweep and its direction (increasing or decreasing frequency) of each FM tone pulse are shown by the horizontal position of the arrow and its intensity by the vertical position. The solid arrow represents the threshold intensity for a given neurone. The arrow with the interrupted line shows an FM tone pulse which did not evoke any impulses at any available intensities. The dotted arrow shows the 'upper threshold' of a neurone which did not respond to an FM tone pulse stronger in intensity than the 'upper threshold'. *D*. Distribution of ranges of best frequencies in octaves in thirty-four single punctures, in which 103 units were recorded.

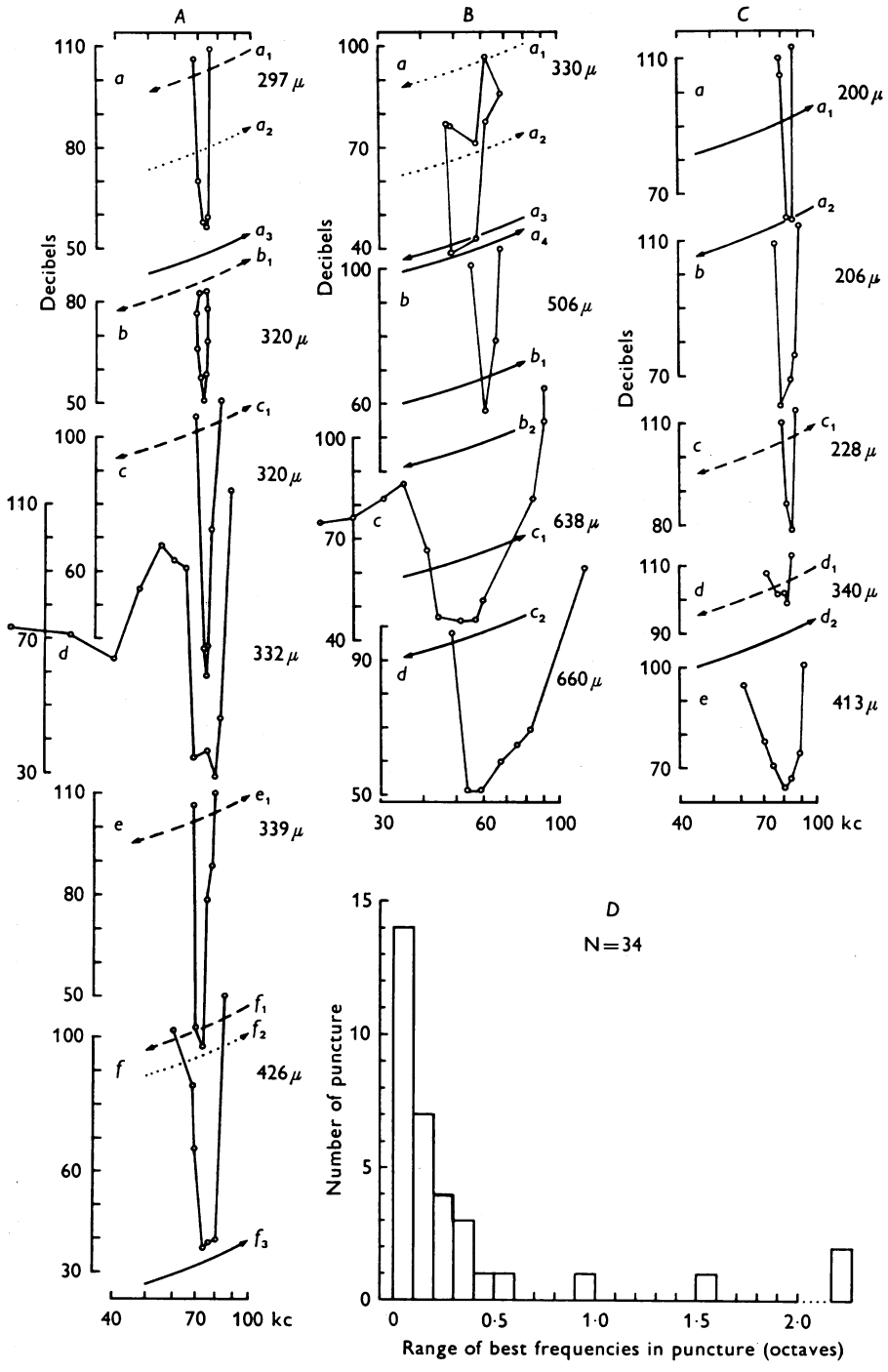


Fig. 3. For legend see opposite page.

roughly perpendicular to the cortical surface. In puncture A, six units were obtained. Unit 'a' at 297 μ was most sensitive to 74 kc tone pulse and was not excited by an FM tone pulse sweeping downward from 100 to 50 kc (arrow a_1) but by an upward sweeping one in the intensity range indicated between arrows a_2 and a_3. Unit 'b' at 320 μ had a 'closed' response area with the best frequency at 73 kc. This neurone was not excited at all by either FM tone pulses of increasing or decreasing frequency (arrow b_1). After disappearance of this unit, impulses of another neurone were recorded without the advancement of the electrode (neurone 'c'). The best frequency of this unit was 75 kc and responses to FM tone pulses sweeping downward or upward between 40 and 100 kc were absent (arrow c_1). The next unit, 'd' at 332 μ was most sensitive to an 80 kc tone pulse. The response area extended over low frequencies and showed two peaks in sensitivity. Neurone 'e' at 339 μ had a narrow response area with the best frequency of about 73 kc and did not respond to any FM tone pulses of any available intensity sweeping between 45 and 100 kc (arrow e_1). The best frequency of neurone 'f' at 426 μ was 74 kc. This neurone did not respond to an FM tone pulse sweeping from 100 to 50 kc (arrow f_1) but responded to an FM tone pulse of increasing frequency at a certain range of intensities (between arrows f_2 and f_3). The deviation of the best frequencies of these six units was very small, 73–80 kc, only 0·1 octave. In this puncture, responses of the neurones to FM tone pulses either were absent or were very much affected by the direction of frequency sweep.

In puncture B, the best frequencies of four neurones ranged from 50 to 60 kc in spite of the different widths of their response areas. In puncture C, the best frequencies of five units were between 80 and 86 kc and their minimum thresholds were higher than those in puncture A. In order to have a statistical view of the extent to which units in the same puncture exhibited similar best frequencies, the range from the lowest to the highest best frequency observed in each puncture was expressed in octaves as in Hind's data (1960). Figure 3D shows the distribution of these ranges in thirty-four punctures in which best frequencies of two or more neurones were measured at different depths. In 62% of these, the range of best frequencies was less than 0·2 octaves. Only about 15% of the punctures showed ranges of more than 0·5 octave. Since the work of Mountcastle (1957) on the somatic sensory cortex, a columnar organization in sensory cortices of cats has been found by Hind (1960) and Parker (1962) in the auditory cortex, and by Hubel & Wiesel (1962, 1963) in the visual cortex. This pattern of organization is also evident in the auditory cortex of bats.

Units recorded in each perpendicular puncture seemed to be similar not only in best frequency, but also in minimum threshold. Figure 4A shows the mean value of minimum thresholds (open circles) and highest

and lowest minimum thresholds (short horizontal bars) observed in thirty-four single punctures. There is a tendency for each puncture to be characterized by a different minimum threshold, although a deviation of more than 20 db from the mean value occurred in a few punctures. In order to calculate a standard deviation of minimum thresholds in single punctures, the deviation of minimum thresholds from the mean value of minimum thresholds obtained in each puncture was plotted on the abscissa of Fig. 4*B*. The ordinate represents the number of units. The histogram, composed of 103 units obtained in thirty-four punctures, gave a standard deviation of 8·5 db. Thus each cortical column consists of units with minimum thresholds which show a standard deviation of only 8·5 db.

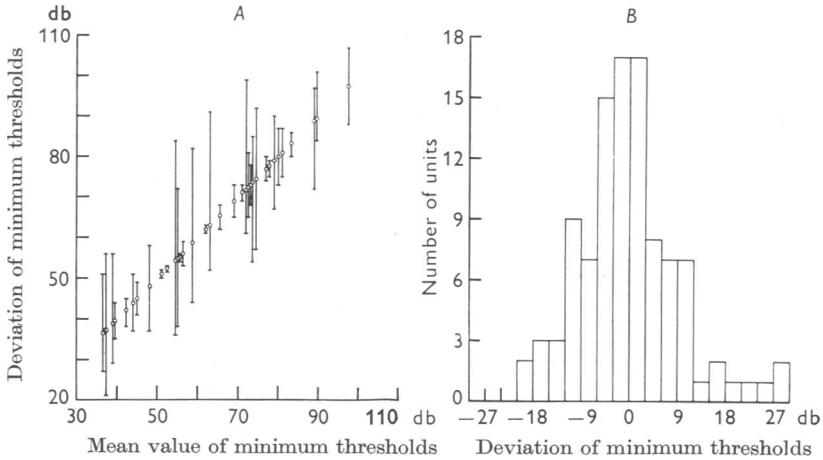


Fig. 4. *A*. Deviation of minimum thresholds in thirty-four single punctures. Open circles represent average values while the short horizontal bars indicate the range of values encountered. *B*. Distribution of deviation of minimum thresholds of 103 neurones from the mean minimum thresholds in thirty-four single punctures. S.D. 8·5 db.

Shape of response areas to pure tone pulses and responses to FM tone pulses

Of the 140 response areas studied, four types could be defined in terms of shape. One type showed two peaks in sensitivity which were separated by an insensitive region (Fig. 5*A*). The minimum threshold was always found at the higher of the two frequencies. In most neurones, there was no sign that an inhibitory area intervened between two sensitive regions. When FM tone pulses swept from the best frequency of a given neurone to an insensitive area or vice versa, neurones of this type showed no difference in threshold. For example, neurone '*a*' in Fig. 5*A* had the minimum threshold at 47 kc and the secondary minimum at 22 kc. The

threshold for an FM tone pulse sweeping up from 30 to 60 kc was the same as that for an FM tone pulse sweeping down within the same frequency range (arrow a_1).

The second type had a wide response area, as shown in Fig. 5*B*. Neurones with such wide response areas had no inhibitory areas and again showed no difference in threshold for FM tone pulses with different directions of frequency sweep (Fig. 5*B*). There was no evidence that these units behaved differently for FM and pure tone pulses from those with wide response areas in the inferior colliculus (Suga, 1965).

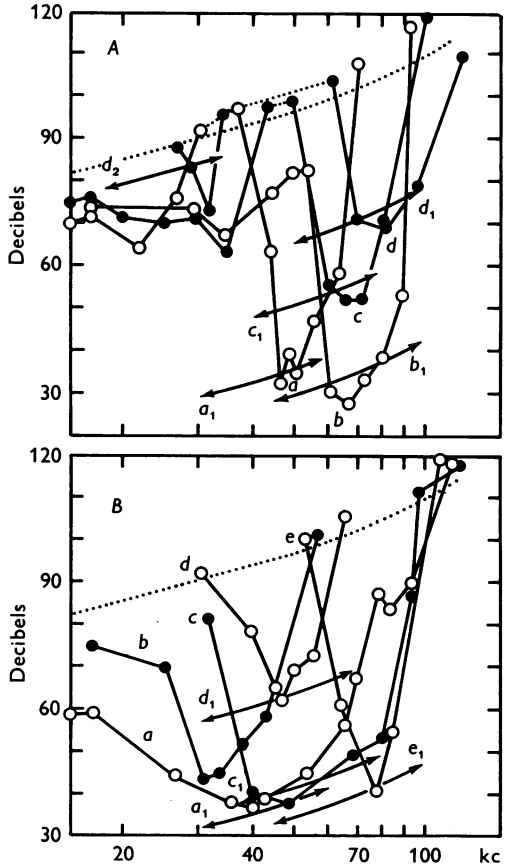


Fig. 5. Response areas and thresholds to FM tone pulses of nine neurones with either areas with two minima (*A*) or wide response areas (*B*). The long dotted line represents the maximum available intensity for FM tone pulses. (Symbols have the same meaning as in Fig. 3.)

Neurones with narrow response areas were the third type, several examples of which are shown in Figs. 3 and 7. This type of neurone behaved

differently for FM tone pulses sweeping across the response area depending on the direction and range of frequency sweep. Some neurones responded to upward but not to downward sweeping pulses (Fig. 3, *Aa*, *Af* and *Cd*; Fig. 7*B*). But others were more sensitive to downward than to upward sweeping FM tone pulses (Fig. 3, *Bb*, *Bc* and *Ca*). Some of these neurones showed upper thresholds, i.e. responses were not evoked by FM tone pulses of high intensity, but were elicited by weak FM tone pulses (Fig. 3, *Aa*, *Af* and *Ba*; Fig. 7*B*). And some neurones with narrow response areas did not respond to FM tone pulses sweeping across the response area at all, although they had a low threshold for pure tone pulses (Fig. 3, *Ac*, *Ae* and *Cc*; Fig. 7*A*).

Four units out of 140 showed 'closed' response areas; these constituted the fourth type of neurone. Spike-count functions of these neurones were non-monotonic, and no impulses at all were evoked by a sound of strong intensity. The response areas were measured by defining as a threshold the weakest intensity which evoked on the average 0·1–0·2 impulses per tone pulse, and on this basis several 'closed' areas were demonstrated (Fig. 3, *Ab* and *Ba*; Fig. 8, *A* and *B*). No responses to any FM tone pulses which swept across their response areas or outside them were found in two of these neurones with closed response areas (Fig. 3, *Ab*). But, neurone '*a* in Fig. 3*B* discharged impulses to either downward or upward sweeping FM tone pulses (arrows a_1 and a_2). It was clear that those neurones with narrow or closed response areas had inhibitory areas at one or both sides of the response area (Fig. 7) or in the strong intensity region (Fig. 8).

Inhibitory areas and responses to FM tone pulses

Responses of neurones with narrow or closed response areas to FM tone pulses were variously modified by interaction between excitation and inhibition as in the inferior colliculus (Suga, 1965). Cortical auditory neurones were usually not spontaneously active. Inhibitory areas were therefore measured with a pair of tone pulses (Fig. 6). One of them was a 4 msec pure tone pulse of a frequency and intensity, chosen to evoke impulse discharges in the given neurone (Fig. 6, 1, lower trace). This pulse is called the *fixed tone pulse*. The other, a 4 msec pulse (hereafter called the *test tone pulse*) was delivered starting 2 msec before the start of the fixed tone pulse (Fig. 6, 2, upper trace) and its effect on impulse discharges was studied by changing its frequency and intensity. Inhibitory areas were then plotted, bounded by threshold intensities at which the test tone pulse just inhibited the response to the fixed pulse, as in Fig. 6, 2. In Fig. 7, two examples of inhibitory areas are given. In *A*, a neurone with a narrow response area did not respond to any FM tone pulses sweeping between 45 and 100 kc. Inhibitory areas (shaded), which were measured with a

fixed tone pulse of 73·1 kc, 46 db, sandwiched the response area. This type of neurone usually failed to respond to click sounds. In *B*, the neurone did not respond to FM tone pulses sweeping down from 100 to 50 kc (arrow 1). But, when the FM tone pulse swept from 80 to 40 kc, responses did appear. The threshold to this pulse was 40 db below the maximum available intensity (arrow 3). Responses to FM tone pulses sweeping up

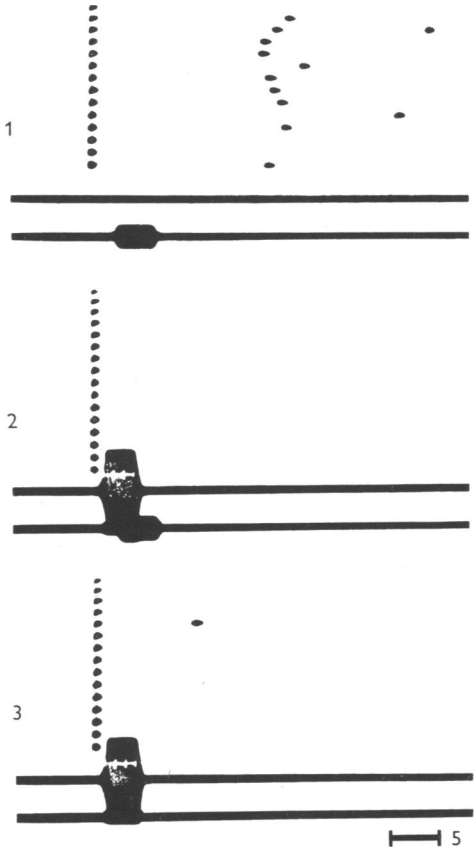


Fig. 6. Response to a fixed tone pulse (1) is inhibited by a test tone pulse (2) which is outside the response area and does not evoke any impulse discharge (3). The dots at the left are electrical markers showing when a tone pulse was delivered, and the elongated dots to the right correspond to nerve impulses. The time scale is 5 msec. Acoustic delay in air (1·8 msec) is not corrected.

from 50 to 100 kc were observed between 24 and 54 db below the maximum available intensity (arrows 2*a* and 2*b*). Inhibitory areas (shaded) measured with a fixed tone pulse of 73·5 kc, 62 db appeared at both sides of the response area. In minimum threshold the inhibitory area to the right of the response area was about 20 db lower than the excitatory area and it abutted on the response area, while the inhibitory area to the left of the

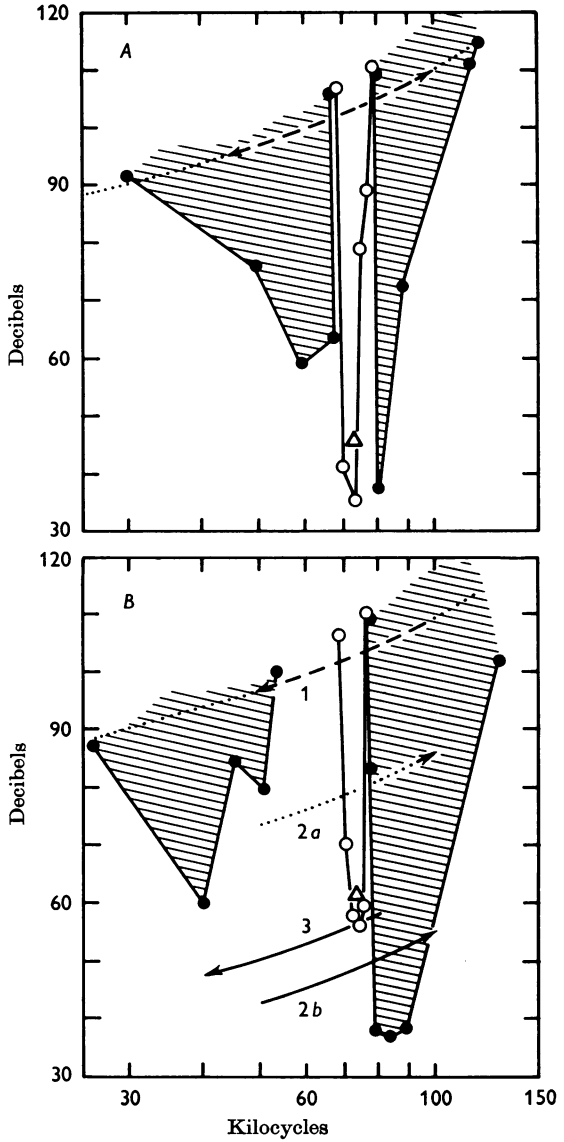


Fig. 7. Excitatory (open circles) and inhibitory (shaded) areas, and responses to FM tone pulses of two single neurones, *A* and *B*. In *A*, the response area is sandwiched between the inhibitory areas, which were measured with a fixed tone pulse of 73·1 kc, 46 db (triangle). The neurone does not respond at all to FM tone pulses. In *B*, the inhibitory areas are asymmetrical at both sides of the response area. The neurone showed an upper threshold and asymmetry in thresholds to FM tone pulses, depending on the direction of frequency sweep. The fixed tone pulse was 73·5 kc, 62 db (triangle). (Symbols have the same meaning as in Fig. 3.)

response area was separated from the excitatory area and its threshold was not lower than that of the excitatory area. As in the inferior colliculus (Suga, 1965), such responses to FM tone pulses were better explained by the sequence of sound stimulating first the excitatory and then the inhibitory areas, rather than by postulating some complex vibration mode of the basilar membrane in the cochlea.

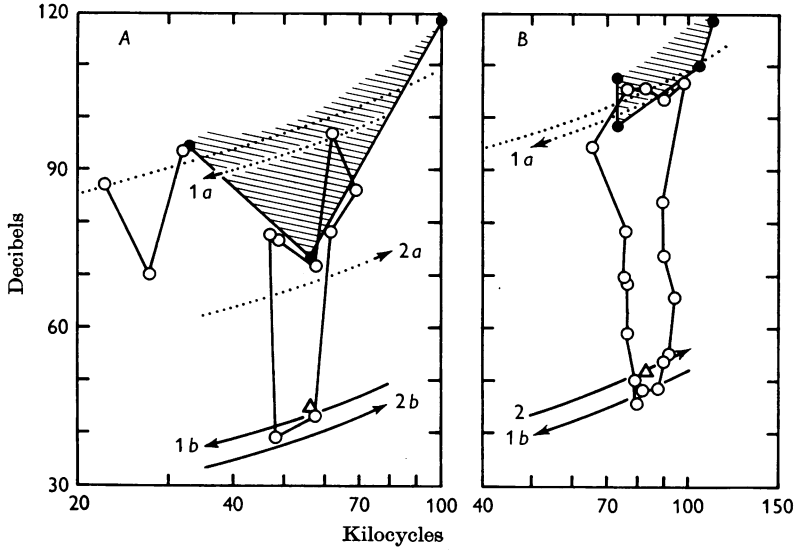


Fig. 8. Two units with 'closed' response areas had inhibitory (shaded) areas at intensities higher than the response areas, and showed upper thresholds to FM tone pulses. The fixed tone pulse was 56·4 kc, 45 db in *A* and 82·7 kc, 52 db in *B*. (Symbols have the same meaning as in Fig. 3.)

Inhibitory areas were measured in two neurones with 'closed' response areas, as shown by shaded areas in Fig. 8. In Fig. 8*A*, the frequency range of the inhibitory area was from 32 to 100 kc at the maximum available intensity. The threshold of inhibitory area at 56 kc was 73 db. It was impossible to continue the measurement of the area because the impulses disappeared, but the area explains the neural basis of a 'closed' response area. This neurone had two response areas shown by open circles. The thresholds for FM tone pulses sweeping between 35 and 80 kc were almost the same (arrows 1*b* and 2*b*), while there was a 26 db difference between upper thresholds owing to the direction of frequency sweep (arrows 1*a* and 2*a*). In Fig. 8*B*, an inhibitory area was located in the high intensity region. An upper threshold appeared for a downward sweeping FM tone pulse (arrow 1*a*). The lack of response to strong FM tone pulses in neurones with closed or narrow response areas did not mean that these neurones had

no inputs. When excitatory pure tone pulses were delivered after these FM tone pulses, the responses to the pure tone pulses were always inhibited. By changing the interval between two tone pulses, it was ascertained that the inhibitory period lasted more than 20 msec after these 4 msec FM tone pulses.

Since inhibitory areas differed in minimum threshold, best frequency, and width as is also the case with excitatory areas, interaction between excitation and inhibition occurred in various ways, and different types of responses of FM tone pulses were produced as discussed below. In some neurones, best frequencies for excitatory and inhibitory areas were separated by more than two octaves, so that interaction between excitation and inhibition could not occur with tone pulses sweeping only one octave.

Neurones more sensitive to FM than to pure tone pulses

Some units which had relatively high threshold response areas were more sensitive to FM than to pure tone pulses. Five examples are given in Figs. 9 and 10. In Fig. 9*A*, the neurone had a U-shaped response area.

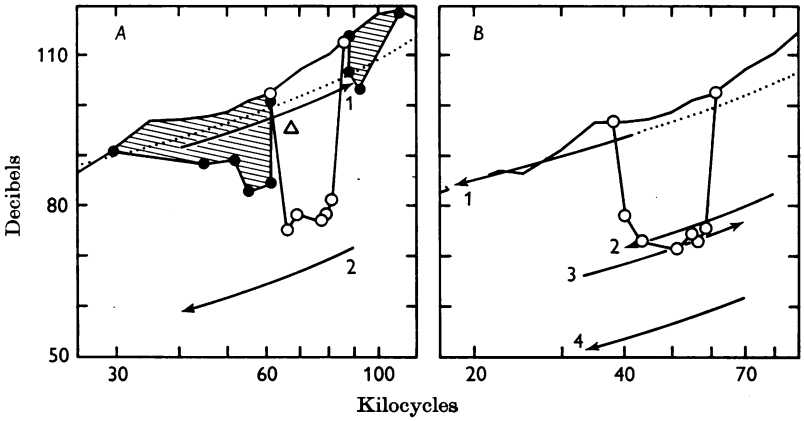


Fig. 9. Two units which showed lower thresholds to FM than to pure tone pulses (arrow 2 in *A* and 4 in *B*). The uppermost solid and dotted lines represent the frequency response curves of the loudspeakers for pure and FM tone pulses respectively. (Symbols have the same meaning as in Fig. 3.)

The FM tone pulse sweeping upward from 40 to 90 kc had almost no excitatory effect on the neurone at the maximum available intensity (arrow 1). This was probably because the inhibitory area was stimulated first. But the downward sweeping pulse was 10 db more effective for this neurone than any pure-tone pulses (arrow 2), in spite of the small number of sound waves falling in the response area. The pure tone pulse was attenuated 30 db below the maximum available intensity (uppermost

solid line) and its frequency was slowly changed, but no frequency effective for this neurone was found at this intensity.

In Fig. 9*B*, the response area is also U-shaped. The thresholds for both FM tone pulses sweeping from 80 to 40 kc and from 33 to 70 kc were almost the same as those for pure-tone pulses (arrows 2 and 3). When the FM tone pulse swept down from 70 to 33 kc, a clear difference between thresholds for the FM and pure-tone pulses appeared (arrow 4). An FM tone pulse sweeping from 40 to 18 kc was almost ineffective at the maximum available intensity (arrow 1).

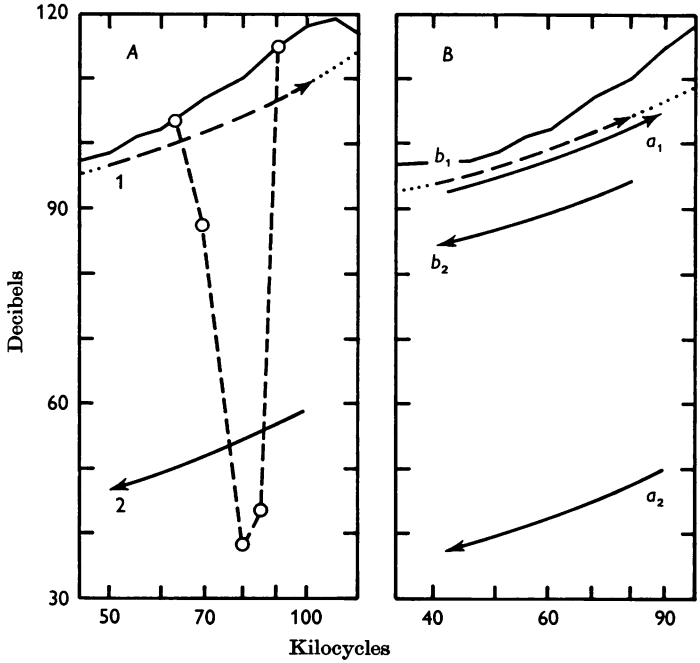


Fig. 10. In neurone *A* there was no response area using the criterion that threshold was the weakest intensity to evoke 0·1–0·2 impulse per tone pulse on the average. But the neurone responded clearly to a downward sweeping FM tone pulse and not to an upward sweeping one. When the criterion of threshold was lowered to 0·05 impulses per tone pulse, the response area shown by open circles and interrupted lines was obtained. In *B*, thresholds of two neurones (*a* and *b*) to FM tone pulses are shown. These neurones had no response areas to pure tone pulses. (Symbols have the same meaning as in Figs. 3 and 9.)

In Fig. 10*A*, the responsiveness of the neurone for pure-tone pulses was so low that a response area could not be measured by the usual criterion of threshold, which was the weakest intensity to evoke an average of 0·1–0·2 impulses per tone pulse. An FM tone pulse sweeping down from 100 to 50 kc, however, evoked 1–2 impulses in this neurone, and the threshold

for this FM pulse was 50 db below the maximum available intensity (arrow 2). No responses to FM tone pulses sweeping upward within the same frequency range were observed (arrow 1). Since there was a 'silhouette' of a response area around 80 kc, the measurement of the response area was attempted with a different criterion of threshold. This was the weakest intensity of sound to evoke 0·05 impulse per tone pulse. The measurement would not have been successful if this neurone had been spontaneously active. The response area measured with this new criterion is shown by open circles and interrupted lines in Fig. 10*A*.

In Fig. 10*B*, thresholds of responses of two neurones '*a*' and '*b*' to FM tone pulses were shown (a_1 and a_2; b_1 and b_2). The threshold was lower for the downward than for the upward sweeping FM tone pulses. No response areas to pure tones were found for these two neurones, however. The neural mechanism for such units is not known yet.

In the auditory cortex, several neurones were encountered which were excited by neither pure nor FM tone pulses, but which were spontaneously active. Perhaps these neurones are auditory units that would be excited if some suitable complex sound were delivered.

Classification of neurones in terms of responses to FM tone pulses

Various types of responses to FM tone pulses have been described above. These were not unique types found only in the cortex, but some were more common in the cortex than in the inferior colliculus. Six categories of cortical units were defined in terms of responses to FM tone pulses sweeping across the best frequency: (1) symmetrical units, (2) asymmetrical units, (3) upper threshold units, (4) FM-insensitive units, (5) FM-sensitive units, (6) high-responsiveness units. As shown in Table 1, eighteen neurones had properties fitting more than one category.

(1) Symmetrical units (about 47 %): Responses to FM tone pulses were not affected by the direction of frequency sweep. Neurones with wide response areas and most units with response areas showing two minima (Fig. 5) belonged to this category and did not show any properties of (2)–(6). These neurones seemed to be concerned simply with registering presence or absence of a particular range of frequencies.

(2) Asymmetrical units (about 27 %): Responses to FM tone pulses differed more than 10 db in threshold depending on the direction of frequency sweep. Some of these units also showed one of the other properties (3), (5) and (6) (Fig. 7*B*). Mode of change in sound was very important for these neurones.

(3) Upper threshold units (about 11 %): These responded to weak but not to strong FM tone pulses. Some neurones with closed response areas were a part of this group (Fig. 8). It has been supposed that such units

may not respond to outgoing orientation sounds, but selectively to weak echoes reflected back by objects at long distances (Hartridge, 1945; Grinnell & McCue, 1963). However, echoes coming back from short distances may not excite these neurones, because a long inhibitory period (more than 20 msec) was produced by the strong stimulus.

(4) FM-insensitive units (about 15%): In these units, no responses to FM tone pulses were found, although the units responded to pure tone pulses of more than 20 db below the maximum available intensity (Fig. 7*A*). FM-insensitive units were so frequency specific that only pure tone pulses within a narrow frequency band excited them. When sounds outside the response area were delivered before, simultaneously with, or even slightly later than the excitatory sound, the responses of the neurones were inhibited. These neurones may be especially useful to detect small objects which produce an echo containing only a high frequency part of the frequency sweep. The response areas of asymmetrical, upper-threshold and FM-insensitive units were commonly narrow (Figs. 3 and 7).

TABLE 1. Classification of neurones in terms of responses to FM tone pulses. Column *A* shows number of units belonging to each category. Column *B* represents eighteen other asymmetrical neurones which also showed one of the other types of properties, upper-threshold (7 units), FM-sensitive (9 units) and high-responsiveness (2 units)

Type of units	*A*	*B*	%
(1) Symmetrical	49	—	46·6
(2) Asymmetrical	10	(18)	9·5 (26·7)
(3) Upper-threshold	5	7	11·4
(4) FM-insensitive	16	—	15·2
(5) FM-sensitive	5	9	13·3
(6) High-responsiveness	2	2	3·8
Subtotal	87	18	—
Total	105		100·0

(5) FM-sensitive units (about 13%): Thresholds of responses of these units were more than 10 db lower to FM than to pure tone pulses, or else responses were evoked only by FM tone pulses. Thresholds of these units for pure tone pulses were commonly high; and their response areas were relatively narrow or U-shaped (Fig. 9), or did not exist at all (Fig. 10). Nine of fourteen units were asymmetrical with respect to FM tone pulses. This is important in understanding the underlying neural mechanism of FM-sensitive units (see Discussion).

(6) High-responsiveness units (about 4%): The number of impulses per tone pulse was more than two times higher to FM than to pure tone pulses, but thresholds to the FM tone pulses were no lower than the minimum threshold measured with pure tone pulses. The percentage of these units was small as shown in Table 1. But the present experiments emphasized thresholds for FM and pure tone pulses. More high-responsiveness units

might be found if numbers of discharges for pure and FM tone pulses were compared. Four of the units listed were found because of noticeable differences in discharge rate. In these neurones the maximum number of impulses per pure tone pulse was at most 0·5–0·8, but it was 1·0–2·0 for the FM tone pulses. Response areas of two of these units were wide, and thresholds to FM tone pulses were the same regardless of whether the pulses were of increasing or decreasing frequency (e.g. Fig. 5*B*, *c*). In the other two, response areas were narrow and inhibitory areas were found at both sides of the response areas. Therefore thresholds to FM tone pulses differed more than 10 db depending on the direction of frequency sweep.

The question might be asked why the FM tone pulses sweeping across both inhibitory and excitatory areas could evoke more impulses than the pure tone pulses could, and furthermore how units unresponsive to pure tone pulses could respond to the FM tone pulses. The neural mechanisms were not studied by attempting to analyse the characters of all presynaptic fibres leading to a particular FM-sensitive unit, but it is possible to make a reasonable interpretation by postulating simple neural networks made up of units with characteristics of those actually found in these bats (see Discussion).

Echo-locating sounds of the bat, *Myotis lucifugus*, always decrease frequency within each short tone pulse. Therefore, it might be expected that neurones more sensitive to downward than to upward sweeping FM tone pulses would predominate. The most effective direction of sweep for exciting a neurone sometimes differed with the range of frequency sweep. In the cortex 22 units were downward-sensitive and 12 upward-sensitive. In the inferior colliculus, 12 were downward-sensitive and 6 upward-sensitive.

Responses to FM tone pulses and width of response areas

The relation between the width of the response area and response to FM tone pulses has previously been studied in the inferior colliculus (Suga, 1965). For comparison of the two levels of the brain, Q values of response areas were calculated for 140 cortical units (Fig. 11). The Q value is, as before, defined as the best frequency divided by the band-width of the response area at 10 db above the minimum threshold. The sharpness of these areas is not adequately expressed by the Q value, since the shapes of the response areas are not a simple triangle, but show abundant variety. There was no sign that the proportion of wide response areas increased compared with that in the inferior colliculus as in the cat (Katsuki, Watanabe & Maruyama, 1959). The open circles in Fig. 11 represent the distribution of Q values of units studied with FM tone pulses. The shaded areas represent that of units which showed other than symmetrical proper-

ties to FM tone pulses. There was a tendency for more variety of response to FM tone pulses to be found in units with narrower response areas, and 28 % of units with Q values less than 8·0 showed other than symmetrical properties to FM tone pulses as shown by the shaded areas in Fig. 11. The shaded areas consisted of 53 % of the cortical units studied with FM tone pulses (Fig. 11). In the inferior colliculus, there was the same tendency as in the cortex, but only 4 % of units with Q values less than 8·0 showed

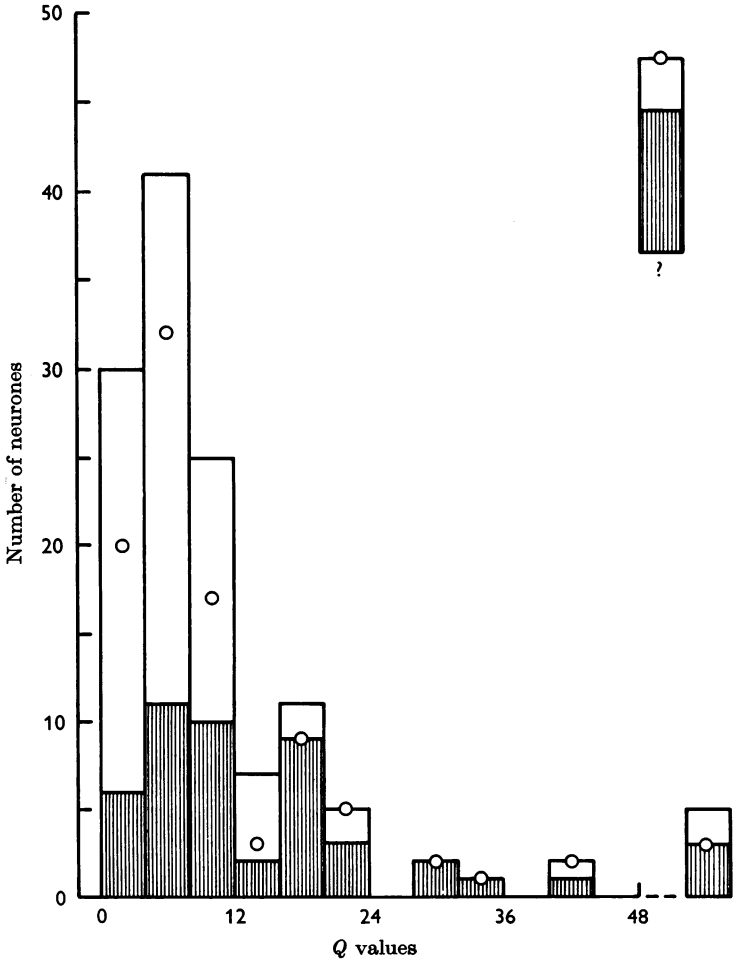


Fig. 11. Distribution of Q values of 140 cortical neurones. In 11 neurones studied with FM tone pulses, the measurement of Q value was not possible owing to high thresholds or lack of responses to pure tone pulses (upper right column). Open circles represent the distribution of Q values of 105 units studied with FM tone pulses and shaded areas that of 56 units which showed special behaviour to FM tone pulses.

various responses to FM tone pulses, and 28 % of the units studied with FM tone pulses composed the shaded areas (Suga, 1965). This difference shows further interaction among neurones at levels higher than the inferior colliculus.

DISCUSSION

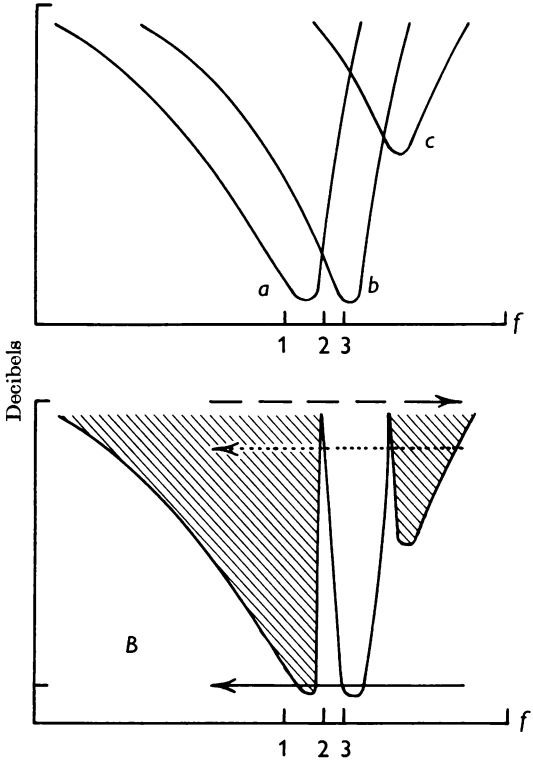
Neural models to explain responses to FM tone pulses

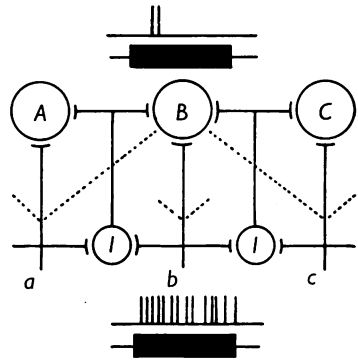
Unlike units in the cochlear nucleus, neurones in the inferior colliculus showed 'phasic' on responses and commonly had non-monotonic spike-count functions. Collicular units with narrow response areas showed different responses to FM tone pulses, depending on the direction and range of frequency sweep. Asymmetrical, FM-insensitive and upper threshold units, as defined above, made up 28 % of collicular units studied (Suga, 1965). In the auditory cortex, more neurones (53 %) than in the inferior colliculus responded in one of several specialized ways to FM tone pulses. Some of these neurones were more sensitive to FM than to pure tone pulses. Such selective responses can be explained by simple neural models, that is, postulated combinations of neurones having the same properties as those actually observed.

The characteristics of asymmetrical, upper-threshold and FM-insensitive units can be accounted for by the neural network shown in Fig. 12. For simplicity let us consider only three lower level neurones, '*a*', '*b*' and '*c*', with the response areas shown in the upper left graph. Neurone '*B*', at the higher level, represents a cell that receives an excitatory input from neurone '*b*' and inhibitory inputs from neurones '*a*' and '*c*' through inhibitory interneurones '*I*' (diagram at upper right). A sound of frequency f_1 stimulates neurone '*a*' much more strongly than '*b*', so that the inhibitory bombardment arrives at '*B*' at the same time or even earlier than the excitatory input from '*b*'. Thus, neurone '*B*' does not respond to f_1, i.e. the response area is sharpened at the low end and an inhibitory area appears as shown by the lower left graph. It may be expected that the inhibitory bombardment through interneurones is more delayed than the direct excitatory input and that therefore the initial part of the excitatory bombardment is not inhibited. This may be true when there is no difference in sensitivity to f_1 between neurones '*a*' and '*b*'. But when the sensitivity of the inhibitory channel is higher than that of the excitatory, such a delay by the interneurone is easily overcome, because the latency of response is changeable as a function of stimulus intensity, especially when the rise time of the stimulus in intensity is slow as in the orientation sounds of these bats.

With a sound of frequency f_3, however, '*b*' is much more strongly stimulated than '*a*' and '*c*', hence neurone '*B*' is excited at first, and then its

discharges are inhibited by the delayed inhibitory bombardment from neurones '*a*' and '*c*' when the intensity of the sound is high enough to stimulate them. But there is no delayed inhibition when the intensity is low. Thus the threshold of neurone '*B*' for f_3 is almost the same as that of '*b*'. But the spike-count function of '*B*' becomes non-monotonic.





Stim-ulus	Channel		
	a	*b*	*B*
f_1	*I*	e	*I*
f_2	*I*	*E*	0
f_3	*i*	*E*	*E*
→ FM	*I*	→ *E*	0, *I*
← FM	*I*	← *E*	*E*

Fig. 12. Neural network producing a narrow response area, non-monotonic spike-count function and phasic 'on' response (upper right). Lower level neurones '*a*', '*b*' and '*c*' (for example, cochlear nucleus) show tonic responses and have response areas shown by the upper left-hand curves. Each of these neurones excites the corresponding higher level neurone, *A*, *B*, or *C*, but inhibits adjacent neurones through inhibitory interneurones (*I*). The lower right table shows the effect of impulses from neurones '*a*' and '*b*' on neurone '*B*' and the resulting responses of neurone '*B*' to each of the pure-tone pulses, f_1, f_2 and f_3. *E* and *e* signify strong and weak excitation, *I* and *i*, strong and weak inhibition respectively. O: no effect at all. As a result of these interactions, neurone '*B*' has a narrow response area and inhibitory areas (lower left graph). The spike-count function becomes non-monotonic at f_3. The response to FM tone pulses changes depending on the direction of frequency sweep. The channels of recurrent inhibition make the response pattern the phasic 'on' response. If there are excitatory inputs from adjacent channels as shown by dotted lines (upper right), the response area of neurone '*B*' would be wide.

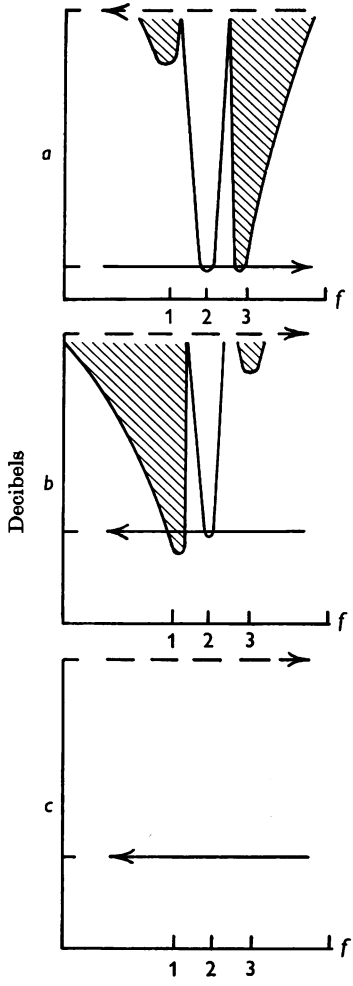
Around frequency f_2, the effects of the excitatory and inhibitory bombardments cancel or weaken each other. The inhibitory bombardment from adjacent neurones is necessary to produce narrow response areas and non-monotonic spike-count functions. Collicular units show generally phasic 'on' responses irrespective of the width of the response area. Such a response pattern is easily produced by a recurrent inhibition. Neurone *B* of Fig. 12 responds to a downward but not to an upward sweeping FM tone pulse, depending on the different sequence of sound stimulating the inhibitory and excitatory areas (Fig. 12, lower left graph). If neurone '*c*' has a short latency compared with '*b*', neurone '*B*' may not be excited by strong sounds of frequencies higher than f_3 but only by weak ones, and may show upper thresholds to downward sweeping FM tone pulses. Different combinations of lower level neurones with various best frequencies, minimum thresholds and latencies make upper level neurones asymmetrical in different ways or insensitive to FM pulses. Furthermore, upper threshold units are produced by much more extensive overlapping of inhibitory areas on a response area than that indicated in Fig. 12.

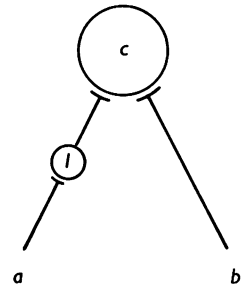
If there are excitatory inputs from neurones '*a*' and '*c*' to neurone '*B*' as shown by the dotted lines in the upper right scheme of Fig. 12, the response area of neurone '*B*' may become wide, but the non-monotonic spike-count function and phasic 'on' response pattern are not affected by these excitatory channels.

FM-sensitive units and high-responsiveness units which had narrow response areas and showed asymmetrical responses to FM tone pulses are not explained by a neural network such as Fig. 12, but rather by the interaction of two such neurones as neurone '*B*' of Fig. 12. As shown in Fig. 13, if neurone '*c*' receives inhibitory and excitatory bombardments from two asymmetrical neurones which are differently sensitive to sweep direction and differ in minimum threshold (upper left two graphs), '*c*' does not respond at all to the pure-tone pulses of frequencies f_1, f_2, and f_3, because of the relatively higher threshold of excitatory channel '*b*' than inhibitory channel '*a*'. For an upward sweeping FM tone pulse, only the inhibitory channel '*a*' affects neurone '*c*'. For a downward sweeping FM tone pulse, there are, however, no inhibitory bombardments from channel '*a*', but excitatory ones of neurone '*b*'. Neurone '*a*' may give the same result on neurone '*c*' even if '*a*' is an FM-insensitive unit which responds only to pure-tone pulses. In this case, responses of neurone '*c*' to FM tone pulses are almost the same as those of neurone '*b*' irrespective of asymmetry or symmetry.

Units with higher thresholds for pure than for FM tone pulses are also explained by two channels, excitatory and inhibitory ones as in Fig. 13.

When the response area of neurone '*b*' in Fig. 13 is slightly wider than that of neurone '*a*', neurone '*c*' has a small response area around frequency f_1 or f_3, because there is no inhibitory bombardment from channel '*a*' for f_1 or f_3. But the thresholds of neurone '*c*' to FM tone pulses are almost the same as those of neurone '*b*' as in Fig. 13. Thus neurone '*c*' shows lower thresholds for FM than for pure tone pulses. Such an explanation means that FM-sensitive units are produced by total or partial deletion of the





Stim-ulus	Channel		
	a	*b*	*c*
f_1	0	0	0
f_2	*I*	e	0, *I*
f_3	0	0	0
→ FM	*I*	0	*I*
← FM	0	E	E

Fig. 13. Neural network to explain FM-sensitive units which have no response area for pure tone pulses. When lower level neurones '*a*' and '*b*' have the properties demonstrated by graphs *a* and *b* and are connected to neurone '*c*' as shown by the upper right diagram (*I*: an inhibitory interneurone), neurone '*c*' responds to FM, but not to pure tone pulses. (Symbols have the same meaning as in Fig. 12.)

response area due to inhibition, but does not mean that FM-sensitive units are produced by the summation of excitatory bombardments.

The alternative explanation for FM-sensitive units may be the summation of excitatory bombardments sent from many neurones, but the difference between thresholds for pure and FM tone pulses seemed to be too large to be explained by summation (Figs. 9 and 10). Psychological experiments show that the binaural threshold is about 3 db lower than the monaural threshold (Licklider, 1951). Improvement of threshold by the summation of excitatory bombardments might not be more than a few decibels.

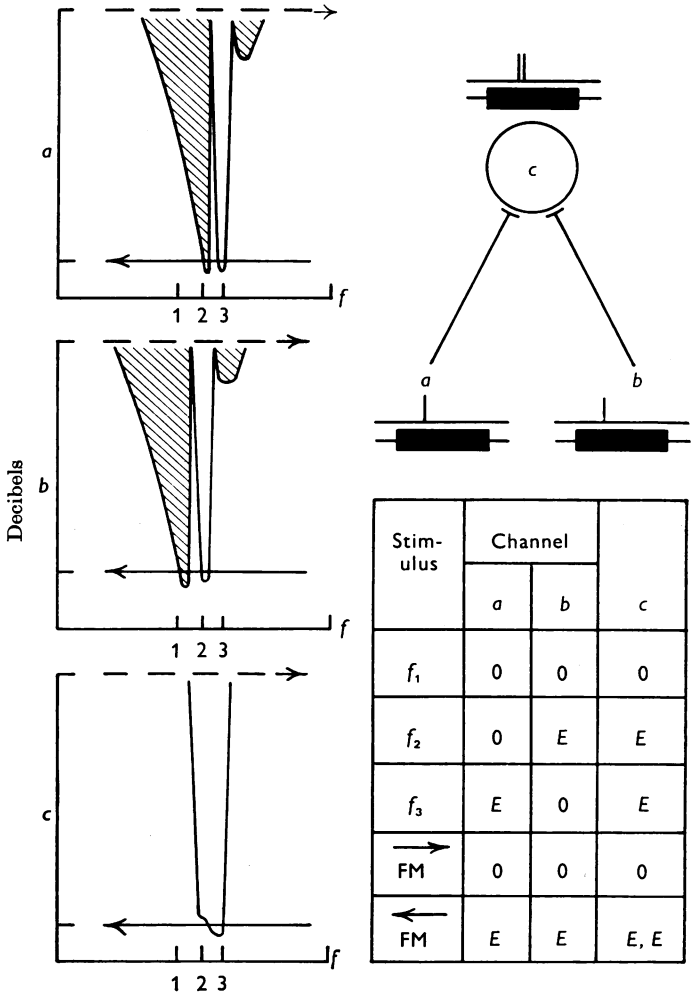
High-responsiveness units with narrow response areas and inhibitory areas showed asymmetry in threshold to FM tone pulses. Such units are explained by two excitatory channels consisting of asymmetrical units (Fig. 14). In Fig. 14, the response areas of two neurones '*a*' and '*b*' are slightly different in frequency, and they are not fully excited simultaneously by any pure-tone pulses, but by downward sweeping FM tone pulses, which may evoke more impulses than any pure tone pulses do (see the table in Fig. 14), but the threshold to the FM pulse may be almost the same as that of neurone '*a*'. Thus FM and some high-responsiveness units are probably produced by interaction among both asymmetrical and FM-insensitive units. In other words, FM-sensitive and high-responsiveness units with asymmetrical characteristics are probably in a higher order of the auditory system than the others. As in Figs. 13 and 14, convergence of neurones with similar best frequencies seems to make the explanation easy. Such convergence may be provided by the columnar organization in the auditory cortex.

Comparison of bat and cat auditory systems in terms of discharge patterns and response areas

Despite the limitations in the validity of comparison between experiments performed under different conditions, units in the cochlear nucleus of bats seem to have less spontaneous activity than those of the cat (Suga, 1964*a*, *b*; Katsuki, Watanabe & Suga, 1959). Units with after-discharges have not been described in cats, but have been in bats (Suga, 1964*a*). There are probably no noticeable differences in the cochlear nucleus in terms of response areas.

In the inferior colliculus, the response pattern seems to be a more phasic 'on' response in the bat than in the cat (Grinnell, 1963; Suga, 1964*a*, *b*; Rose *et al.* 1963). Tonic units are rare in the inferior colliculus of bats. The shape of the response areas has been well studied systematically from the cochlear nucleus to the auditory cortex in cats (Katsuki *et al.* 1958; Katsuki, Watanabe & Maruyama, 1959). Katsuki and co-workers (1958, 1959)

showed progressive sharpening of the response area with ascent from the cochlear nucleus to the inferior colliculus and geniculate body. On the other hand, Erulkar (1959) described two types or response areas, wide and narrow, in the cat's inferior colliculus. Furthermore, the response areas described by Rose *et al.* (1963) are not always narrow as described



Stim-ulus	Channel		
	a	*b*	*c*
f_1	0	0	0
f_2	0	E	E
f_3	E	0	E
→ FM	0	0	0
← FM	E	E	E, E

Fig. 14. Neural network to explain high-responsiveness units with asymmetrical properties. When neurone '*c*' receives excitatory bombardments from both neurones '*a*' and '*b*' which have characters as shown by the upper two graphs on the left, the response area of neurone '*c*' becomes slightly wider than either of the two input channels. None of the pure tone pulses f_1, f_2 and f_3 activate both channels simultaneously but a downward sweeping FM tone pulse does. The responsiveness of neurone '*c*' is higher for the FM than for pure tone pulses. (Symbols have the same meaning as in Fig. 12.)

by Katsuki *et al.* (1958). In the bat, widths of response areas were not necessarily narrower, but were wider in some neurones than those of the cochlear nucleus (Suga, 1964*a*, 1965). Therefore, there may be no qualitative difference between the two animals in terms of response areas.

Response patterns in the auditory cortex are phasic 'on' responses in both animals (Erulkar *et al.* 1956; Katsuki, Watanabe & Maruyama, 1959; Hind, 1960), although slightly different results were obtained in unanaesthetized cats (Galambos, 1960; Kiang, Neame & Clark, 1961; Evans & Whitfield, 1964*a*). The response areas in the cat's cortex are much wider than those of the medial geniculate body, resembling more the units of the cochlear nucleus (Katsuki, Watanabe & Maruyama, 1959). In the bat, the width of response areas in the auditory cortex did not seem to change noticeably from those in the inferior colliculus. No comparable experiments with FM tone pulses have been performed in any animals other than bats. In terms of responses to FM tone pulses, units with narrow response areas in the inferior colliculus and auditory cortex of bats seem to be differentiated to analyse the changes in sounds. Neurones with wide response areas, on the other hand, were relatively insensitive to changes in sound. If this is true in the cat's cortex where most neurones have wide response areas, the cat's auditory cortex may be less suited for the analysis of complex sounds than the bat's cortex. The cortex is, however, necessary for the discrimination of temporal patterns of tones (Diamond & Neff, 1957; Golgberg *et al.* 1957). According to Katsuki, Watanabe & Maruyama (1959), the response area of auditory neurones in the cat became narrowest at the medial geniculate body and became widest in the auditory cortex by the convergence of the geniculate neurones on cortical ones. If this is the case, cortical neurones may show complex responses which have not been described in the bats. Quite recently, Evans & Whitfield (1964*b*) have presented preliminary reports of cortical neurones in the cat selectively sensitive to FM tone pulses of either increasing or decreasing frequency.

It is difficult clearly to define the auditory mechanism which is responsible for the remarkable echo-location of bats. The difference in auditory neurones between echo-locating and non-echo-locating animals may not be qualitative, but quantitative. There are no comparative electrophysiological data concerning the central auditory systems of various animals. In the visual system, there are, however, interesting neurophysiological data obtained from various animals (Hubel & Wiesel, 1959, 1962; Lettvin, Maturana, Pitts & McCulloch, 1961; Maturana & Frank 1963; Barlow, Hill & Levick, 1964). In the cat, neurones capable of differentiating the movement of a spot of light are found only in the visual cortex (Hubel *et al.* 1959, 1962), but such units are found at the optic nerve level in the frog (Lettvin *et al.* 1961), pigeon (Maturana & Frank, 1963) and rabbit

(Barlow *et al.* 1964). In the echo-locating bats, where the relay nuclei below the medial geniculate body are enormously developed, the importance of mid-brain relay nuclei including the inferior colliculus for echo-location has been suggested from the anatomical viewpoint (Poljak, 1926; Zvorykin, 1959). It may be reasonable to suggest that as a result of 'neurobiotaxis' the phasic units with either very wide or narrow response areas are more commonly found in the levels lower than the cortex as opposed to the cat, and the relay nuclei of lower levels perform more complex processing of information than those of the cat do. The comparison between units in the inferior colliculus and auditory cortex showed that more cortical neurones behaved differently to FM tone pulses than did collicular ones. Cortical auditory neurones probably take a role in the further fine analysis of complex sounds.

SUMMARY

1. The auditory cortex of echo-locating bats was studied by recording evoked potentials and single unit activity with glass micropipette electrodes. In the auditory cortex, located at the temporal region of the cerebrum, neurones sensitive to high frequencies were located anteriorly and those to low frequencies posteriorly. Within single punctures perpendicular to the cortical surface, the neurones recorded had similar best frequencies and minimum thresholds which varied with a standard deviation of 8·5 db.

2. Various types of response areas were obtained: wide, narrow, and closed areas, and areas with two minima. Neurones with wide areas or areas showing two minima commonly showed the same responses to FM tone pulses of increasing or decreasing frequency. But those with narrow or closed response areas responded differently to FM tone pulses depending on the direction of frequency sweep. There was no tendency for the response area in the auditory cortex to be wider than that in the inferior colliculus.

3. Neurones were classified into six groups according to their responses to FM tone pulses: symmetrical, asymmetrical, upper-threshold, FM-insensitive, FM-sensitive, and high-responsiveness units. Responses of neurones other than symmetrical ones to FM tone pulses were explained by the sequence in which excitatory and inhibitory areas were stimulated.

4. The population of asymmetrical, upper-threshold, FM-sensitive, FM-insensitive, and high-responsiveness units made up 53 % of neurones studied in the auditory cortex; in the inferior colliculus the corresponding percentage was 28.

5. Neural models are described which would produce the various types of responses encountered in the bat cortex. FM-sensitive units can be explained more readily by postulating inhibitory interaction between two

asymmetrical neurones than by calling upon augmentation due to the summation of excitatory bombardments from many neurones.

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