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ANALYSIS OF FREQUENCY-MODULATED AND COMPLEX SOUNDS BY SINGLE AUDITORY NEURONES OF BATS

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SUMMARY

1. Single unit activity in the inferior colliculus of bats was studied in relation to the analysis of frequency-modulated (FM) and complex sounds. Complex sounds were composed of tone pulse I (pure or FM tone) delivered simultaneously with tone pulse II (pure or sometimes FM tone). It was assumed that in relevant complex sounds produced by animals, an important component (e.g. a formant in human speech) occurred at the best frequency (BF) of a given neurone. Tone pulse I represented such a component (called BF component). Tone pulse II was assumed to correspond to higher or lower components according to its relation to BF. Depending on characteristics of responses to tonal stimuli, collicular neurones were classified into five types: symmetrical, asymmetrical, FM-insensitive, FM-sensitive (or FM-specialized) and upper-threshold units.

2. The symmetrical unit had a wide excitatory area and no inhibitory areas and it responded with equal thresholds to FM tone pulses sweeping in either directions. This type of neurone responded to all frequency modulations (e.g. transition in human speech) of the BF component, and the response was scarcely inhibited by other components.

3. In the asymmetrical unit, the extent of frequency modulation of the BF component which could excite the neurone was limited by inhibitory areas on one or both sides of an excitatory area. Inhibitory areas on the lower frequency side tended to be larger than those on the high frequency side. The limitation was more severe for frequency sweeps toward the best frequency than for sweeps starting from it. The response to the BF component was inhibited by lower and/or higher components unless these were outside the inhibitory areas. In most of the asymmetrical units, lower components were more important than higher ones in determining whether the response to the BF component could occur.

4. In the FM-insensitive unit with a narrow excitatory area, inhibitory

areas on both sides of the excitatory area restricted the extent of frequency modulation of the BF components which could activate the neurone. Responses to frequency sweeps toward the best frequency were strongly limited by the inhibitory areas. When the lower and/or higher components were within the inhibitory areas, the response to the BF component was inhibited. This type of neurone responded to more restricted combinations of components than did the asymmetrical units.

5. The FM-sensitive unit which had no excitatory area but a large inhibitory area responded only to FM components in a certain range. Evidence was obtained that not only the range and direction but rate and functional form of frequency sweep were important in determining the excitation of the neurone. Noise bursts with various band widths did not activate the neurones. Responses of the neurones were commonly inhibited by tones within an inhibitory area so wide as to involve even frequencies in the FM component which excited the neurone. Thus, the response of the FM-sensitive unit depended not only upon the characteristics of the FM component, but also on the frequencies of other components.

6. The asymmetrical, FM-insensitive and FM-sensitive units required for their activation a certain structure in the complex sound. Some of the upper-threshold units did not respond to a sufficiently strong BF component and/or its frequency modulation. Furthermore, the response of the neurone to a weak BF component was inhibited by strong lower and/or higher components in a certain range. Some upper-threshold units also had asymmetrical or FM-sensitive characteristics. Those neurones appeared to be specialized for the analysis of sound structure not only in frequency, but in intensity.

7. Although various types of behaviour of single neurones were found in the inferior colliculus, a strong tendency in the neural analysis of complex sound was the restriction of conditions under which single neurones were activated. Neurones at higher levels responded to more restricted sequences or sets of sound stimuli than did those at lower levels.

INTRODUCTION

For acoustic communication, mammals and birds produce a variety of sounds whose frequency and intensity change with time. These are generally complex sounds consisting of several frequencies. Human speech contains particularly complex sounds. Here many different phonemes are combined in different sequences in order to convey information. However, psychoacoustical experiments have shown that words can be perceived correctly even when few components of the original phoneme remain (e.g. Flanagan, 1965).

In order to study the neural analysis of complex sounds by recording single unit activity, there are at least two methods for delivering stimuli. One is to use tape-recorded complex sounds, some components of which are filtered or modified. The other is to combine two or three simple artificial stimuli, each of which resembles a component of a natural sound to be mimicked. Since activity of single auditory neurones was first recorded by Galambos & Davis (1943), many experiments on activity of single neurones have been performed with pure tone bursts and clicks, and qualitative and quantitative data on characteristics of responses of single auditory neurones have been accumulated. However, little effort has been made to explore responses of single neurones to complex sounds including human speech and to understand the neural analysis of complex sounds in which many parameters change with time. The lack of such an attempt may be due to the complexity of sound and to the absence of detailed analysis of information-bearing elements in the communication sounds of animals. In human speech, however, these elements are known, although speech recognition is accomplished not only by acoustic cues, but also by linguistic, semantic and circumstantial cues. Therefore, a useful first step in studying the neural analysis of complex sounds is experiments on responses of single units to sounds similar to those elements.

Speech spectra show three essential patterns: (1) resonance (or horizontal) bars called 'formants' which are spectral peaks characterizing vowels or vowel-like sounds, (2) 'fills' in which sound energy distributes over a wide range of frequency and which characterize consonants, and (3) slopes or curves of resonance bars which appear in transition from one phoneme to another, which are called 'transitions' (Potter, Kopp & Kopp, 1966). These three patterns may be called (1) pure tone (constant frequency) components, (2) noise bursts, and (3) FM (frequency-modulated) components because frequency changes with time. These components are also found in sounds produced by animals.

Some experiments with pure tone bursts seem to give an answer to the question how each pure tone component of complex sounds is analysed by the neural network. For example, Katsuki and his co-workers show that the frequency sensitivity of single neurones is sharpened by inhibition with ascent from the cochlear nucleus to the geniculate body (Katsuki, Sumi, Uchiyama & Watanabe, 1958; Katsuki, Watanabe & Maruyama, 1959; Katsuki, Watanabe & Suga, 1959). This suggests that the higher centres of the auditory system have neurones which respond only to a certain formant of the vowels or vowel-like sounds. Although click sounds, which are to some extent similar to 'spike fills' (fills with a short duration), have often been used especially in the study of sound localization, few systematic experiments have been performed which clarify the neural analysis of the fills. In cat auditory cortex, the presence of neurones which responded only to noise bursts was reported (Galambos, 1960; Evans & Whitfield, 1964).

When a vowel or vowel-like sound is connected with other phonemes as in words, the formants of the sound are affected by the phoneme preceding or following it and the transitions appear between the phonemes. How then do the neurones, which are presumably tuned to analyse certain formants, respond to such a transition? Experiments with FM sounds demonstrate that some neurones in the inferior colliculus (Suga, 1964*b*; 1965*a*) and auditory cortex (Suga, 1965*b*, *c*; Whitfield & Evans, 1965; Nelson, Erulkar & Bryan, 1966) respond differently to FM sound depending on the direction and range of frequency sweep. Furthermore, some neurones do not respond to pure tone bursts at all, but only to certain FM sounds. These experiments suggest that the central auditory system has neurones which can analyse the transition.

In vowels and vowel-like sounds, there are more than three formants which are called the 'first' 'second', 'third',...formants from the lowest one. The first two or three formants are information-bearing components which have the strongest influence on speech recognition. In identifying sound pattern and sound combination in a sonagram, the major cue is the relation of the second formant to the first and third formants (Potter *et al.* 1966). Plosive and some fricative consonants are recognized by the transitions of the second formant of the vowels. The importance of the transition of the second formants as a cue in speech recognition must be emphasized (Cooper, Delattre, Liberman, Borst & Gerstman 1952; Liberman, Delattre, Cooper & Gerstman, 1954; Liberman, 1957; Heinz & Stevens, 1961). Therefore, the responses of neurones to the transition (FM sound) have to be explored in relation to the analysis of human speech. Furthermore, the responses of single neurones to certain formants or transitions must be studied with respect to influences of other formants. These problems are not special for human, but are common for many mammals and birds, because communication sounds used by these also consist of many components including FM.

In order to pursue these two problems, the present experiments are performed with an acoustically specialized animal, the bat, which analyses fine differences of echoes for orientation and discrimination. Responses of single neurones in the inferior colliculus are studied because it has been demonstrated that some of these neurones show special behaviour to FM sounds (Suga, 1965*a*). Various characteristics of single neurones are enumerated, and general principles which may be applicable to the analysis of complex sounds including human speech are discussed on the basis of single neurone activity. Results are presented in three parts: (I) Classification of neurones and their inhibitory areas, (II) Responses to FM tone pulses modulated by various functional forms, and (III) Responses to complex sounds consisting of combinations of pure tone and FM components.

METHODS

Yuma bats (*Myotis yumanensis*) were caught in old houses in southern California. The bats (about 6–7 g) were anaesthetized by intraperitoneal injection of sodium pentobarbitone (45 mg/kg). Ether was used at the initial phase of the operation to stop movement of the animal if necessary. The operation and the recording of single unit activity were carried out in a sound-proofed room at 35–37° C. After cutting away the temporal muscle, a small hole was made in the skull over the inferior colliculus for the insertion of a micro-electrode. The bat was mounted on a small metal plate after the operation. The skull was held fast by four sewing needles fixed on four micromanipulators as in the previous experiments (Suga, 1964*a*).

The glass micropipette electrode filled with 3 M-KCl was mounted on a micromanipulator which was driven hydraulically from outside the sound-proofed room and was inserted into the inferior colliculus. An indifferent electrode was on the neck muscles through wet cotton. Single unit activity was amplified and was displayed on an oscilloscope screen.

In order to simulate the basic properties of some components of human speech or other complex sounds, sound stimuli were generated as follows: a Wavetek voltage-controlled sine wave generator (model 111) was controlled by a home-made sweep-function generator which produced either linearly or exponentially rising or falling voltage. In Fig. 1, 1 and 2, six functional forms for frequency modulation are shown. Functional form 'A' modulates the frequency linearly with time, while functional forms 'B' and 'C' modulate exponentially. In form 'B', low frequencies are included more than in form 'A' (Fig. 1, 4), while high frequencies are accentuated in form 'C' (Fig. 1, 5). The sound modulated by form 'A' is called 'A-FM' tone pulse. The terms, 'B-FM' and 'C-FM' are similarly defined.

The Wavetek generator produced a continuous sine wave, the frequency of which was constant or modulated linearly or exponentially with time according to the voltage from the sweep function generator. In order to have only the frequency modulated or unmodulated portion as shown in Fig. 1, the continuous sine wave was formed into a short electric signal corresponding to a tone pulse by a Grason–Stadler electronic switch driven by pulses synchronizing with the voltage signal from the sweep function generator. The duration and rise-decay time of the tone pulse were kept at 4·0 msec and 0·5 msec respectively, unless otherwise stated (Figs. 1 and 2).

Since the rise-decay time was 0·5 msec in order to reduce transients at the onset and cessation of the tone pulse, the amplitude of the FM voltage to the loudspeaker was not uniform. The relation between frequency modulation and intensity is schematically shown in Fig. 2*A*. In this figure, the frequency of an electric signal with an envelope shown in *a* is modulated by a linearly rising voltage indicated by *b*. The modulation starts and ends when the amplitude of the signal is between 20 and 30 db below the plateau. Therefore, the intensity of this signal changes with frequency sweep as shown by a curve in Fig. 2*A*, *c*. The tone pulse produced by this electric signal is conventionally called an A-FM tone pulse sweeping from 40 to 80 kc/s. The frequency in pure and FM tone pulses was always measured with electronic counters.

The electric signal corresponding to a tone pulse from the electronic switch was amplified by a Hewlet–Packard amplifier (model 450) and a Krohn–Hite power amplifier (model DCA 50) after passing through a General Radio decade attenuator. Finally, the signal drove a solid-dielectric condenser loudspeaker with a 300 V bias potential, through a 40db power attenuator which was used in order to improve the signal-to-noise ratio when the

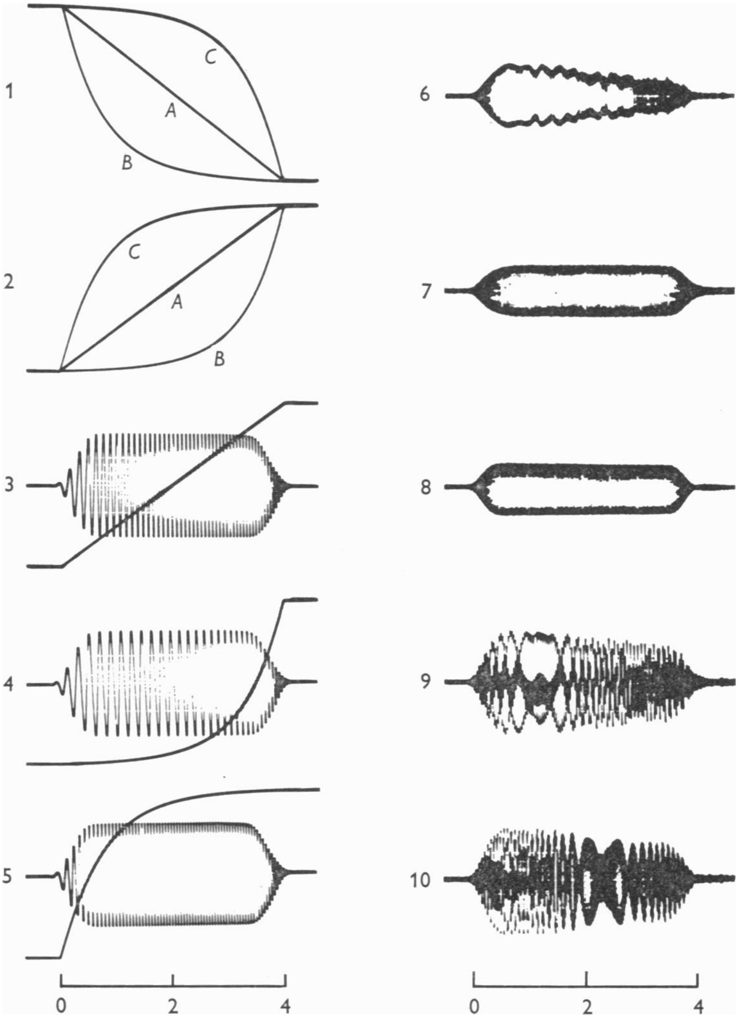

Fig. 1. Sound stimuli used in the present experiment. 1 and 2 show six functional forms used to modulate the frequency of sound. All three functional forms, *A*, *B*, and *C*, modulate sounds from high frequency to low in 1 and from low to high in 2. In 3, 4, and 5, FM tone pulses clearly show the frequency sweep, from 5 to 20 kc/s during 4 msec, in different functional forms. The form is *A* in 3, *B* in 4, and *C* in 5. Sound waves picked up by a calibrated microphone (B and K 4135) placed immediately above a bat's head are shown in 6–10. 6: an FM tone pulse sweeping from 70 to 35 kc/s at about 80 db SPL in functional form *A*. 7: a pure tone pulse of 29 kc/s, 80 db SPL. 8: a pure tone pulse of 50 kc/s, 80 db SPL. 9: the FM tone pulse in 6 is mixed with the pure tone pulse in 7 by simultaneous delivery. 10: the FM tone pulse in 6 is mixed with the pure tone pulse in 8 by simultaneous delivery. Sonagrams of the sounds in 6–10 are shown in Fig. 2*B*.

sound intensity was attenuated more than 40 db. Thus the sound intensity was controlled by both the General Radio decade attenuator and the power attenuator. Stimuli were repeatedly delivered to the animal with a silent interval of 0·5–0·7 sec.

The stimulating system consisted of two identical sets of equipment, as described above, so that two tone pulses which were independently controlled in frequency, intensity, duration, and rise-decay time could be delivered simultaneously (e.g. Fig. 1, 9 and 10) or successively. The time separating two tone pulses was controlled by a Grass stimulator. Two loudspeakers, one above the other, were placed 92·5 ± 0·2 cm from the bat's ears. The sound intensity at the bat's ears was determined with a Brüel and Kjaer calibrated con-

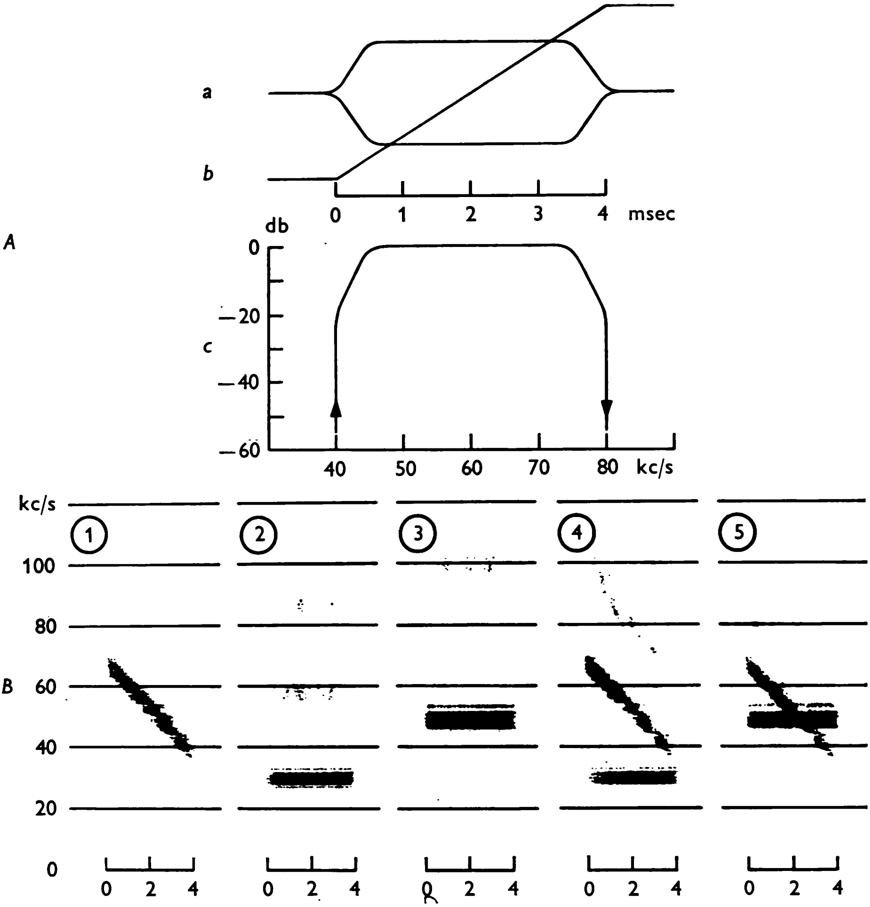

Fig. 2. *A* illustrates the relation between frequency modulation and intensity in FM tone pulse. *a*: envelope of a tone pulse. *b*: voltage change to modulate frequency in functional form *A*. *c*: relation between frequency sweep and intensity of the FM tone pulse. *B* shows the sonagrams of the tone pulses sampled in 6–10 of Fig. 1. 1: the A-FM tone pulse sweeping from 70 to 35 kc/s. 2: the pure tone pulse of 29 kc/s. 3: the pure tone pulse of 50 kc/s. 4: a combination of the FM and 29 kc/s pure tone pulses. 5: a combination of the FM and 50 kc/s pure tone pulses. Harmonics and combination tones present although these are faint.

denser microphone 4135. The solid dielectric condenser loudspeaker could deliver sounds from 25 to 150 kc/s (the frequency–response curve is shown in Figs. 3 and 4). To deliver sounds lower than 25 kc/s, two Ionovac loudspeakers (Duk 5) were used which could deliver sounds from 5 to 50 kc/s. All sound intensities in this paper are expressed in db SPL (sound pressure level) (re 0·0002 dyne/cm^2 r.m.s.). Figure 1, 6–10, shows wave forms of A-FM, pure tone and complex sounds, the last consisting of pure and FM tone pulses, which were monitored by the calibrated microphone. Some of the tone pulses used in the present experiments were analysed by a Kay Electric Co. Sonagraph which accentuated high frequencies in the recording circuit, so that any faint harmonics present were well shown in the sonagrams (Fig. 2*B*). The effective band width of the sonagraph was 4·8 kc/s. When FM and pure tone pulses were mixed in air, combination tones appeared in the sonagram, although these were very faint (Fig. 2*B*, 4 and 5).

Because of the frequency–response curve of the loudspeaker, the intensity within the FM tone pulse was not uniform but varied with frequency even at a constant input voltage to the loudspeaker (e.g. Fig. 1, 6). Therefore, the intensity of the FM tone pulse had to be expressed as attenuation below the maximum intensity available from the loudspeaker, i.e. by a line parallel to the frequency–response curve (see Figs. 3 and 4). However, the intensity of the FM tone pulse is given with the intensity at the centre of its frequency sweep in order to simplify the description.

A threshold for excitation was defined as the lowest intensity of a sound which evoked 0·1–0·2 impulse per tone pulse on the average, while a threshold for inhibition, as that reducing an average rate of impulse discharges higher than 0·5 per tone pulse to less than 0·1 impulse per tone pulse.

PART I

CLASSIFICATION OF NEURONES AND THEIR INHIBITORY AREAS

The neurones may be classified according to either (*a*) the response pattern, (*b*) the best frequency, (*c*) the minimum threshold, (*d*) the *Q* value, which is the best frequency divided by the bandwidth at 10 db above the minimum threshold, or (*e*) according to their responses to FM tone pulses sweeping one octave with the best frequency at the centre of the tone pulses. The last classification is most relevant to this study, and it is used here with the terminology developed for cortical auditory neurones (Suga, 1965*c*). Thus the types of units studied are called 'symmetrical', 'asymmetrical', 'upper-threshold'. 'FM-insensitive' and 'FM-sensitive (or FM-specialized)'. The qualification must be made that some neurones have characteristics belonging to more than one of these types.

Measurement of excitatory and inhibitory areas gives the most basic clues to the analysis of responses to FM and complex sounds. An excitatory area was measured with single pure tone pulses which were different in frequency and intensity, while an inhibitory area was measured with a pair of pure tone pulses as described below. A 4 msec pure tone pulse (hereafter called 'tone pulse II') was delivered before, without overlapping, a 4 msec excitatory pure or FM tone pulse (hereafter called 'tone pulse I'). The frequency (or FM) and intensity of tone pulse I were kept constant, while those of tone pulse II were changed in order to measure an area in which tone pulse II caused inhibition or augmentation of the response to tone pulse I. Since the size and shape of an inhibitory area change depending on the frequency and intensity of the tone pulse I and the larger inhibitory area is obtained with the weaker tone pulse I (Suga, 1965*a*; Figs. 8–11), the weakest excitatory tone pulse available was used as tone pulse I. The intensity was adjusted to evoke one impulse at every other stimulus, so that the inhibition or the augmentation of the response by tone pulse II would be clearly observed if it existed (Fig. 3).

RESULTS

In thirty-nine adult bats, 356 neurones were sampled from the dorsal and central regions of the inferior colliculus. Almost all of these neurones showed phasic on-responses to sound stimuli of 40 or 400 msec duration and showed no spontaneous discharges. Several neurones showed tonic discharges or inhibition of spontaneous discharges during sound stimuli or inhibition during the stimuli and discharges at the cessation. In this paper, characteristics of on-response units are described. The on-responses were usually superimposed on the summit or falling phase of the slow component (the latency of which was 7–9 msec at the peak) of the evoked potential change in the inferior colliculus.

As in *Myotis lucifugus* (Suga, 1965*c*), symmetrical units usually had a wide excitatory area and either no inhibitory area or a very small one. Asymmetrical units had a narrow excitatory area and inhibitory areas on both sides (or one side) of the excitatory area. Inhibitory areas in a given neurone were greatly different from each other in minimum threshold. Upper-threshold units had an inhibitory area or areas which greatly overlapped a narrow excitatory area or were located above a closed excitatory area. FM-insensitive units had a narrow excitatory area which was sandwiched in between inhibitory areas which had similar minimum thresholds. FM-sensitive units had a small excitatory area at a high intensity or no excitatory area at all, but had a large inhibitory area. Since the inhibitory areas of the FM-sensitive units have not yet been described, three examples are shown in Figs. 3 and 4.

In Fig. 3*A*, a neurone had a small excitatory area with the best frequency of 46 kc/s, the threshold for which was 59 db SPL, whereas thresholds to A-FM tone pulses sweeping upward or downward between 35 and 70 kc/s or between 40 and 80 kc/s ranged between 30 and 36 db SPL. Thus, the difference in threshold was more than 23 db. It was confirmed that there was no excitatory area except for that in Fig. 3*A*. Tone pulse II delivered before tone pulse I did not augment, but inhibited the response to tone pulse I. An inhibitory area appeared as shown by a shaded area (Fig. 3*A*). In Fig. 3*B*, a neurone showed 28 db lower threshold to an A-FM tone pulse sweeping from 35 to 70 kc/s than to the pure tone pulse at the best frequency, but did not respond to an A-FM pulse sweeping from 70 to 35 kc/s. When the downward sweeping FM tone pulse was delivered before an excitatory sound such as a pure or upward sweeping FM tone pulse, the response to the excitatory sound disappeared. That is, the downward sweeping FM tone pulse did not excite this neurone, but caused only an inhibitory process. The neurone had a large inhibitory area (Fig. 3*B*). In

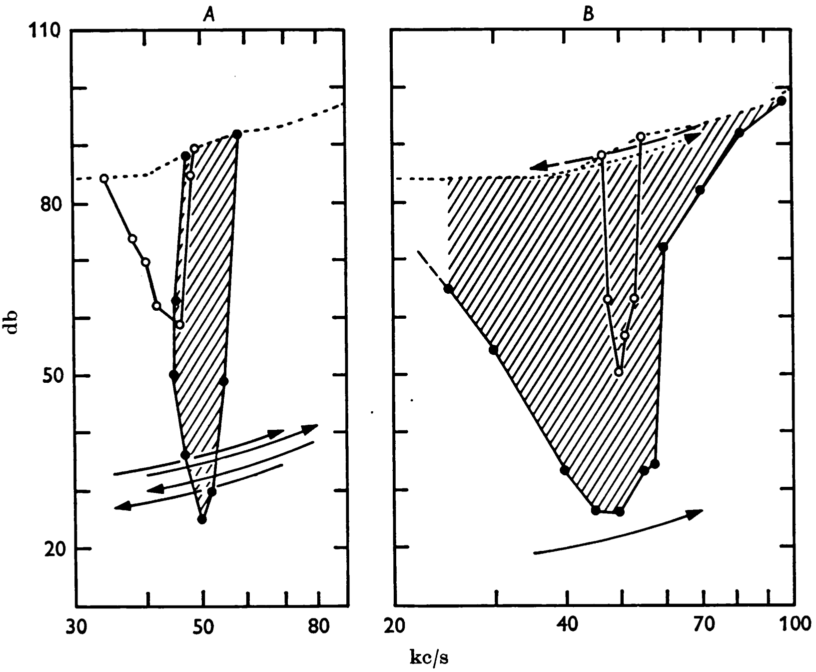

Fig. 3. Inhibitory (shaded) areas of two FM-sensitive units, *A* and *B*, which had small excitatory areas (areas surrounded by open circles). The ordinates and abscissas represent intensity (db re 0·0002 dyne/cm^2 r.m.s.) and frequency (kc/s) of sounds. The inhibitory area was measured by tone pulse II (pure tone) delivered before tone pulse I sweeping from 70 to 35 kc/s at 75 db SPL in *A*, and from 35 to 70 kc/s at 29 db SPL in *B*.

The range and direction of a frequency sweep in an FM tone pulse are shown by an arrow parallel to the frequency–response curve (uppermost dotted line) of one of the condenser loudspeakers, and its intensity, by the vertical position of the arrow. A solid arrow represents the intensity at the threshold for a given neurone. A dashed arrow shows an FM tone pulse which did not evoke any impulses at any available intensities. A 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.'

the shaded area overlapping the excitatory area in Fig. 2*A* and *B*, stimuli were not purely inhibitory but were themselves excitatory while suppressing the response to a second stimulus.

In Fig. 4*B*, a neurone had no excitatory area, but a large inhibitory area. This neurone showed, however, clear responses to FM tone pulses with two impulses per stimulus at the maximum. Measurements on twelve FM-sensitive neurones showed that all except one had a large inhibitory area rather than an area for augmentation. Such results suggest that, in a neural chain between the spiral ganglion cells and these inferior collicular ones, there are inhibitory synapses which are not activated by certain FM tone pulses, but by pure tone pulses.

One neurone with a small excitatory and a large inhibitory area responded to FM tone pulses sweeping upward from the inhibitory to the excitatory area, but not to those sweeping in the opposite direction. The average number of impulses was about 0·7 per pure tone pulse at the maximum and 2·0 per FM tone pulse. The difference in threshold between responses to pure and FM tone pulses was 5 db. Similar units were also found in both the inferior colliculus and auditory cortex of *Myotis lucifugus*. The paradox that the neurones were excited by FM tone pulses sweeping only across an inhibitory area or from the inhibitory to excitatory area could be accounted for as in an earlier explanation of FM-sensitive units (Suga, 1965*c*).

PART II

RESPONSES TO FM TONE PULSES MODULATED BY VARIOUS FUNCTIONAL FORMS

Responses of single neurones with narrow excitatory areas to FM tone pulses vary considerably depending on both the range and direction of frequency sweeps. The difference is explained by the sequence and extent of stimulation of excitatory and inhibitory areas (Suga, 1965*a*, *b*, *c*). Therefore in what functional form the frequency sweeps, appears important for the neurones, especially for FM-sensitive ones. Most transitions in human monosyllables fall in between the functional form B and C (Potter *et al.* 1966). As extreme cases, the six functional forms of Fig. 1 were used for the frequency modulation of tone pulses. Responses of single neurones to these FM tone pulses with different functional forms were studied (Figs. 4 and 5).

In human speech, the extent of transition changes depending on what phoneme is connected with a vowel or vowel-like sounds and in what sequence these are connected. Since it is reasonably assumed that single neurones are most concerned with sounds at their best frequencies (e.g. with such a formant of a vowel that its frequency is the same as the best frequency of a given neurone), responses to FM tone pulses were studied which swept the frequency from or to the best frequency in order to explore how single neurones responded to transitions in various modes. The sound at the best frequency, which was measured in each neurone, was delivered at an intensity of 80 db SPL. It was, then, modified by different functional forms. Either the initial or the final frequency of the tone pulse was always kept at the best frequency of a given neurone (Fig. 6).

Since the rate of transitions changes with both speech speed and combinations of phonemes, responses to FM tone pulses sweeping at different rates were also studied (Fig. 7).

RESULTS

Responses to FM tone pulses with different functional forms of frequency modulation. In Fig. 4*A*, the response of a neurone which had a narrow excitatory area and a large inhibitory area is shown. The neurone did not respond to FM tone pulses of any form sweeping between 25 and 50 kc/s but did respond when the sweep range was between 35 and 70 kc/s. When the sweep range was between 30 and 60 kc/s, the neurone did not respond to an upward sweeping A-FM tone pulse but to a downward sweeping A-FM (A 1). To B-FM tone pulses, which remained at low frequency longer than A-FMs, the neurone did not respond at all (A 2). However, the neurone responded to C-FM tone pulses which included high frequencies more than A-FMs, irrespective of sweep direction (A 3). Both presence and absence of responses could be explained by a balance of excitation and inhibition.

An FM-sensitive neurone in Fig. 4*B* responded to FM tone pulses in more complex ways. To FM tone pulses sweeping between 30 and 60 kc/s, clear responses were obtained only when the functional form was B. In the sweep range from 40 to 80 kc/s, A- and C-FM tone pulses were equally effective on the neurone, except for tone pulses stronger than 60 db SPL. To B-FM tone pulses, the neurone only responded when the direction of sweep was upward (see Fig. 4*B* for more detail). In general, responses of the FM-sensitive neurone were greatly affected by the functional form of frequency modulation.

Two FM-sensitive neurones were found which showed much stronger response to one functional form than to the others for a given sweep range (Fig. 5). However, no FM-sensitive unit has yet been found which responded to only one modulating form and not to any others, in any part of frequency range. Figure 5 shows the effect of change in functional form of frequency modulation on responses of an FM-sensitive unit which had no excitatory area and showed no responses to click sounds. When the frequency of sound swept linearly with time to 32 kc/s, the neurone showed responses

(Fig. 5, 1). No clear responses were obtained to FM tone pulses sweeping exponentially (Fig. 5, 2 and 3). However, clear responses appeared to all of three types of FM tone pulses when the final frequency was 42 kc/s (Fig. 5, 4–6). In the FM tone pulses with a final frequency of 52 kc/s, the neurone responded to pulses with a growing exponential form and poorly or not at all to the other forms (Fig. 5, 7–9). No responses were obtained to any FM tone pulses terminating at 62 kc/s (Fig. 5, 10–12). As far as this measurement was concerned, the neurone was most easily excited by both the linear and growing exponential sweeps of FM tone pulses, but not by the decaying exponential.

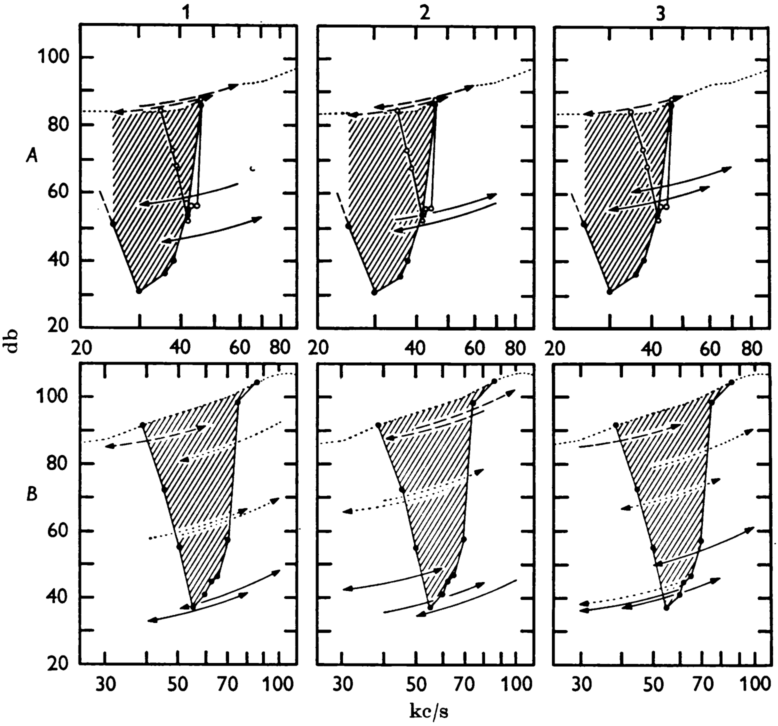

Fig. 4. Responses of two units, *A* and *B*, to FM tone pulses sweeping according to different functional forms. Neurone *A* had an excitatory area, but *B* had not. The inhibitory area was measured by delivering tone pulse II (pure tone) followed by tone pulse I sweeping from 35 to 70 kc/s at 52 db SPL in *A*, and from 80 to 40 kc/s at 45 db SPL in *B*. The functional form of the frequency sweep was '*A*' in 1, '*B*' in 2, and '*C*' in 3. All symbols have the same meaning as in Fig. 3.

Lack of response of the neurones in Fig. 4 to FM tone pulses sweeping in a certain direction and also to those of intensity above the upper threshold did not mean that the neurones received no signal from other neurones under these conditions. They had received an inhibitory bombardment because responses to excitatory sounds were inhibited by the preceding presentation of the FM sounds which did not excite the neurones. For example, the FM tone pulse sweeping from 80 to 40 kc/s did not activate the neurone in Fig. 4, *B*2 and it inhibited responses to other FM tone pulses, e.g. the tone pulse sweeping from 40 to 80 kc/s at 44 db SPL. The threshold for this inhibition (the minimum intensity of the downward sweeping FM tone pulse which caused inhibition) was 38 db SPL, being almost the same as the threshold for the upward sweeping FM tone pulse.

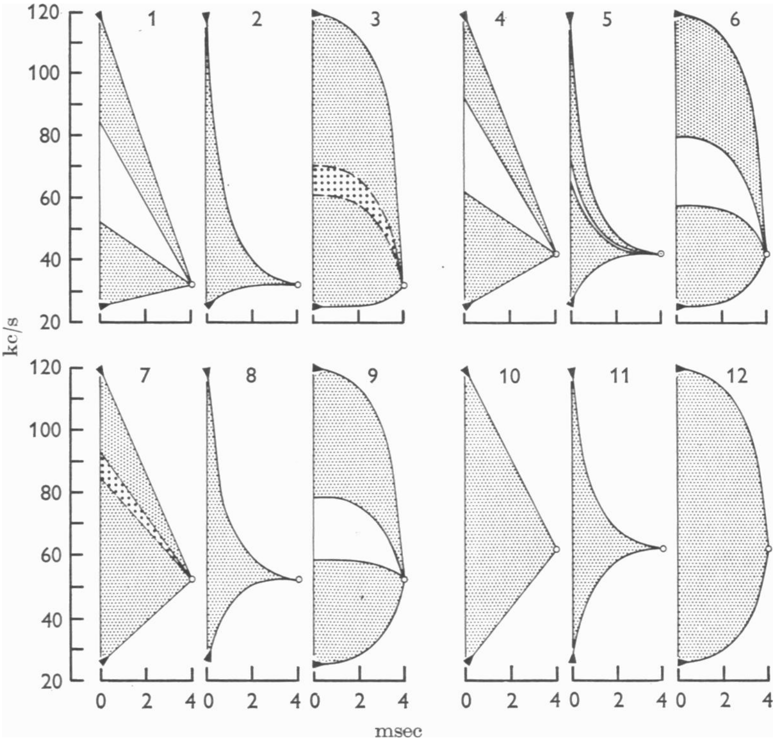

Fig. 5. Responses of an FM-sensitive unit to FM tone pulses sweeping in different functional forms. The ordinates and abscissas represent frequency in kc/s and time in msec, respectively. At first, a pure tone pulse of 80 db SPL was delivered (32 kc/s in 1–3, 42 kc/s in 4–6, 52 kc/s in 7–9, and 62 kc/s in 10–12). It was then frequency modulated by different forms. Keeping the final frequency constant, the initial frequency of FM was changed in order to measure the range where responses were obtained. Densely dotted sectors mean that FM tone pulses in the sectors did not excite the neurone. In the undotted sectors between the dotted ones, FM tone pulses excited the neurone. In lightly dotted sectors, the neurone discharged impulses to FM tone pulses, but the probability of the response was slightly lower than that at threshold defined in this paper. The functional form of frequency sweep is linear in 1, 4, 7, and 10, decaying exponential in 2, 5, 8, and 11, and growing exponential in 3, 6, 9, and 12.

This was also true for other FM tone pulses which did not excite the neurone in certain sweep directions and/or at certain intensities.

Responses to FM tone pulses sweeping from or to the best frequency. In Fig. 6*A*, a neurone had a narrow excitatory area and inhibitory areas (*A* 1). When the frequency swept toward the best frequency, responses of the neurone to A-FM tone pulses were or were not obtained, depending upon the range of the frequency sweep (*A* 2). The neurone responded to A-FM tone pulses sweeping from the best frequency irrespective of sweep range, but responses were slight within the coarsely dotted sectors (*A* 3). The results of similar measurements with FM tone pulses sweeping exponentially were shown in *A* 4–*A* 7. The following results were obtained mainly with A-FM tone pulses.

Symmetrical units responded to any FM tone pulses sweeping to or from their best frequencies. Asymmetrical units with large inhibitory areas below narrow excitatory ones were not activated by FM tone pulses sweeping from low frequencies to their best frequencies, but by the pulses sweeping downward from high frequencies. To FM tone pulses sweeping away from the best frequency, the neurone often showed responses regardless of sweep range. A few asymmetrical units with inhibitory areas at frequencies higher than excitatory ones were found, which were not sensitive to FM tone pulses sweeping from high frequencies to their best frequencies, but to the tone pulses sweeping from low frequencies. It was noticed that one third of asymmetrical units were upward-sensitive and two thirds, downward-sensitive (Suga, 1965*c*). Figure 6*C* gives an example of an asymmetrical unit which showed an upper threshold to the sound at the best frequency. The neurone did not respond to FM tone pulses strongly including the sound of the best frequency and especially to those sweeping away from the best frequency to low frequencies or vice versa.

Responses of FM-insensitive units to the frequency modulation of the sound at the best frequency were more strongly limited by inhibitory areas on both sides of their narrow excitatory areas than the asymmetrical units. Tone pulses frequency-modulated so as to terminate at the best frequency from the outside of the excitatory area usually failed to excite these neurones. The neurones responded only to FM tone pulses sweeping within the excitatory area and to some of the tone pulses frequency-modulated so as to diverge from the best frequency (e.g. Fig. 6*B*).

Since the best frequency was not measurable in FM-sensitive units which had no excitatory areas, an FM tone pulse which was the most effective in exciting a given neurone was at first found by trial. Then the range of frequency sweep was changed by keeping the initial or final frequency of the tone pulse constant. An FM-sensitive unit in Fig. 6*D* responded to either FM tone pulses sweeping upward or downward in a

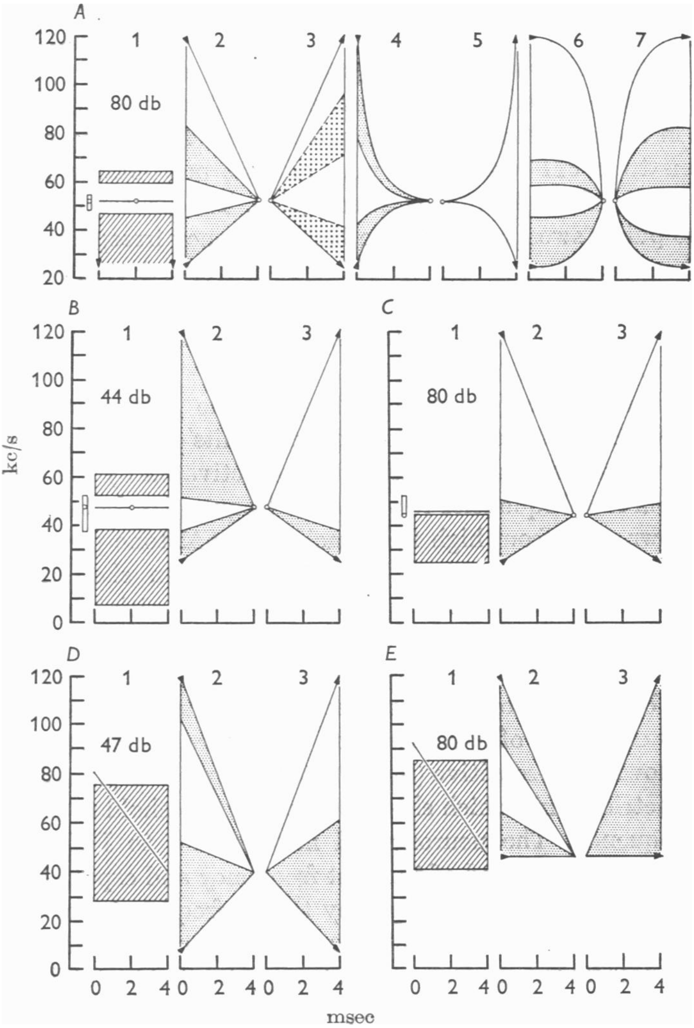

Fig. 6. Responses of five neurones to FM tone pulses sweeping to or from the best frequency. The ordinates and abscissas represent frequency in kc/s and time in msec, respectively. In 1, the width of the excitatory area at 80 db SPL (if any) is shown by a vertical white bar to the left. The open circle in the bar indicates the best frequency. The widths of the inhibitory areas at 80 db SPL are shown by the shaded areas, which were measured by delivering tone pulse II (pure tone) simultaneously with tone pulse I (a pure tone pulse of 52 kc/s, 80 db SPL in *A* 1; 47 kc/s, 44 db SPL in *B* 1; 46 kc/s, 80 db SPL in *C* 1, an A-FM tone pulse sweeping from 80 to 40 kc/s at 47 db SPL in D 1, and an A-FM tone pulse sweeping from 92 to 46 kc/s at 80 db SPL in *E* 1 as shown by a solid line and figures in each graph). The unshaded square (if any) means that tone pulse II in the square increased the number of impulses compared with that for tone pulse I alone. Symbols in 2–7 have the same meaning as in Fig. 5.

certain range, while FM-sensitive neurones in Figs. 6*E* and 11 responded only to certain FM tone pulses sweeping downward. It was clear that responses of certain FM-sensitive neurones were limited not only by sweep range but also sweep direction.

Although it seemed certain from the above results that particular frequency sweeps were necessary for activation of FM-sensitive units, it was

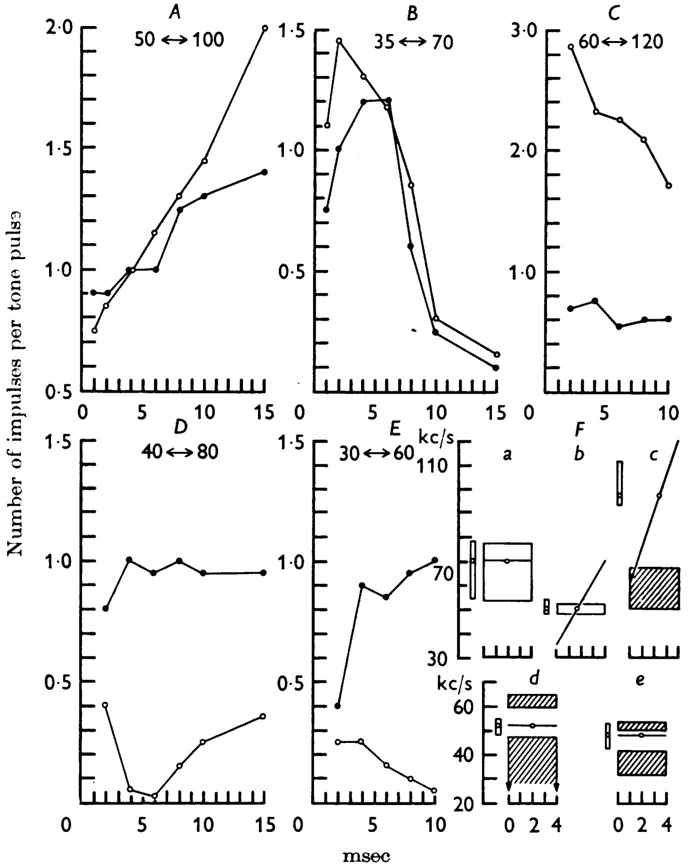

Fig. 7. Responses of five neurones to A-FM tone pulses sweeping in different rates. The A-FM tone pulses of 80 db SPL always swept by an octave across the excitatory area within a time period (i.e. the duration of the stimulus) as shown by the abscissas. The ordinates represent number of impulses per tonal stimulus on the average. The open circle shows the number of impulses in a response to an upward sweeping FM tone pulse, and the filled one, that to a downward sweeping FM. The range of frequency sweep is from 50 to 100 kc/s in *A*, 35 to 70 kc/s in *B*, 60 to 120 kc/s in *C*, 40 to 80 kc/s in *D*, and 30 to 60 kc/s in *E*. In *F*, the widths of excitatory and inhibitory areas at 80 db SPL are shown for five units sampled in *A*–*E*, which correspond to *a*–*e* in *F*. Symbols in *F* have the same meaning as in Fig. 6, 1.

further examined whether these neurones responded to noise bursts in which all frequencies in FM tone pulses were mixed. In two FM-sensitive units with no excitatory areas, no responses to 4 msec noise bursts with various band widths and intensities were found.

Responses to FM tone pulses sweeping at different rates. As expected from Figs. 4 and 6, most neurones showed less response to FM tone pulses sweeping first across inhibitory areas at a lower rate, but better responses to those which first swept across an excitatory area at a slower rate. In FM-sensitive units, an optimum rate of frequency sweep was found to excite them (Fig. 7*B*).

When an FM tone pulse was delivered which swept one octave with the best frequency at the centre of the frequency sweep, various changes in response were observed with the rate of the frequency sweep. In Fig. 7*A*, the average number of impulses per tone pulse increased with the time required for one octave sweep. The frequency range of pure tone pulse which excited this symmetrical unit is shown in Fig. 7, *Fa*. In Fig. 7*B*, an FM-sensitive unit with a small excitatory area shows the best response to an FM tone pulse sweeping from 35 to 70 kc/s in 2 msec, but when the sweep direction is reversed, the most effective rate is one octave per 4–6 msec. The neurone responded poorly to FM tone pulses sweeping slowly. Three examples of asymmetrical units are given in *C*, *D* and *E* of fig. 7. The change in response with the rate of frequency sweep differed in these neurones. In Fig. 7*D*, the minimum response appeared to the FM tone pulse sweeping from 40 to 80 kc/s in 4–6 msec. To the FM tone pulses sweeping slowly in 10–15 msec, the probability of response increased in spite of the fact that many sound waves first fell into the inhibitory area shown in *d* of Fig. 7*F*. This suggests that there are phasic inhibitory neurones and the duration of the inhibitory process is independent of the duration of the stimulus if its duration is longer than a certain limit.

PART III

RESPONSES TO COMPLEX SOUNDS CONSISTING OF COMBINATIONS OF PURE TONE AND FM COMPONENTS

Animals more commonly use complex sound than pure or simple FM tones for communication. In complex sound, a few or many other frequencies co-exist with a pure tone or FM component. Therefore, there is the question whether the responses of the neurones described in the preceding sections of this paper will appear in the presence of other sounds. In other words, the role of inhibitory areas has to be explored not only in terms of the analysis of each element of complex sound, but in terms of the analysis of whole complex sound.

In order to study this problem, two sounds which had the same duration (4 msec) and rise-decay time (0·5 msec) were delivered simultaneously (e.g. Fig. 1, 9 and 10). One, at the best frequency (or FM sweeping from or to the best frequency) of a given neurone at 80 db SPL, was called tone pulse I. The other is tone pulse II (pure tone), the frequency of which was changed, keeping its intensity at 80 db SPL. The range in which tone pulse II caused augmentation or inhibition of the response to tone pulse I was measured. Here augmentation simply means increase in probability of response or in number of impulses caused by delivering tone pulse II, so that the 'augmented response' could be the sum of the responses to each tone pulse, or less (occlusion) or more (facilitation) than the sum. Since neurones in the inferior colliculus commonly showed phasic on-responses, the augmentation of the response to tone pulse I was not always clear (Figs. 8–11).

RESULTS

Responses of non-FM-sensitive neurones to complex sounds. As expected from the experiment in which tone pulse II was delivered preceding tone pulse I, symmetrical units had no range of sounds producing inhibition, (e.g. Fig. 7, *Fa*). In asymmetrical units, inhibitory sounds appeared on one side or both sides of the best frequency (e.g. Fig. 6*C*; Fig. 7*F*, *c*, *d*, and *e*). FM-insensitive units had inhibitory areas on both sides of the best frequency (e.g. Fig. 6, *A* and *B*). In the neurones which showed upper-thresholds to pure tone pulses as well as to FM pulses, responses to certain tone pulses were inhibited even by a sound which fell into the frequency range of sounds excitatory to the given neurones, when its intensity was above the upper-threshold (e.g. Fig. 8*B*). Therefore, whether the response of these neurones listed above to certain components were retained or not depended on the location of the other components of the complex sound, i.e. on the structure in the complex sound.

When an FM tone pulse in which the frequency swept from or to or across the best frequency of a given neurone was delivered as tone pulse I, the range of sound for inhibition changed depending on the FM tone pulses used. Such a change in inhibitory range was to be predicted because the size and shape of inhibitory areas changed as a function of both the intensity and frequency of a sound used as tone pulse I (Suga, 1965*a*). In most neurones, the change was limited in a certain range predictable from the measurement using a pure tone pulse as tone pulse I (e.g. Fig. 8). But, some neurones showed a completely different range of inhibitory sounds to FM tone pulses as compared with that to pure tone pulses (e.g. Fig. 9, *A* and *B*).

Figure 8 shows inhibitory ranges of an asymmetrical (*A*) and an upper threshold unit (*B*). In the asymmetrical unit, the range of sounds which inhibited the response to either a pure tone pulse at a best frequency (*A* 1) or A-FM tone pulses (*A* 3 and *A* 4) always appeared below the range of excitatory sounds, although the width of the range was not the same. In the upper-threshold unit of Fig. 8*B*, responses to pure tone pulses of 80 db

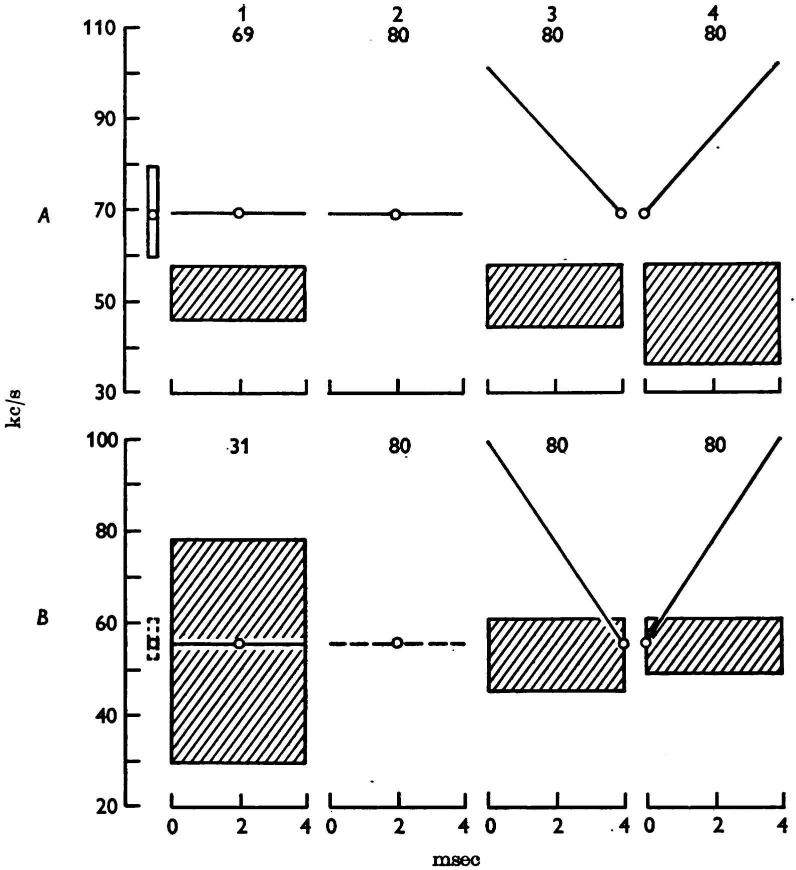

Fig. 8. Responses of an asymmetrical (*A*) and an upper-threshold unit (*B*) to complex sounds. Symbols have the same meaning as in Fig. 6, 1. A dotted vertical bar in *B* 1 represents the width of an excitatory area at 40 db SPL. The neurone responded to 80 db SPL sounds with a probability lower than the criterion of threshold. Tone pulse I expressed by a dashed line means that the neurone did not respond to it.

SPL were below 0·1–0·2 impulse per stimulus on the average, so that the range of inhibitory sounds was not measurable (*B* 2). When a weak sound at a best frequency was used as tone pulse I, a large inhibitory area was, however, obtained (*B* 1). The range of inhibitory sounds for responses to certain FM tone pulses is shown in *B* 3 and *B* 4.

In Fig. 9, three examples are given in which the range for inhibition or augmentation was greatly different depending on the FM tone pulses used as tone pulse I. A neurone in Fig. 9*A* had excitatory and inhibitory areas as shown in *A* 1 and *A* 2. This neurone did not respond to the A-FM tone pulse sweeping from 75 to 50 kc/s. When tone pulse II (pure tone) was

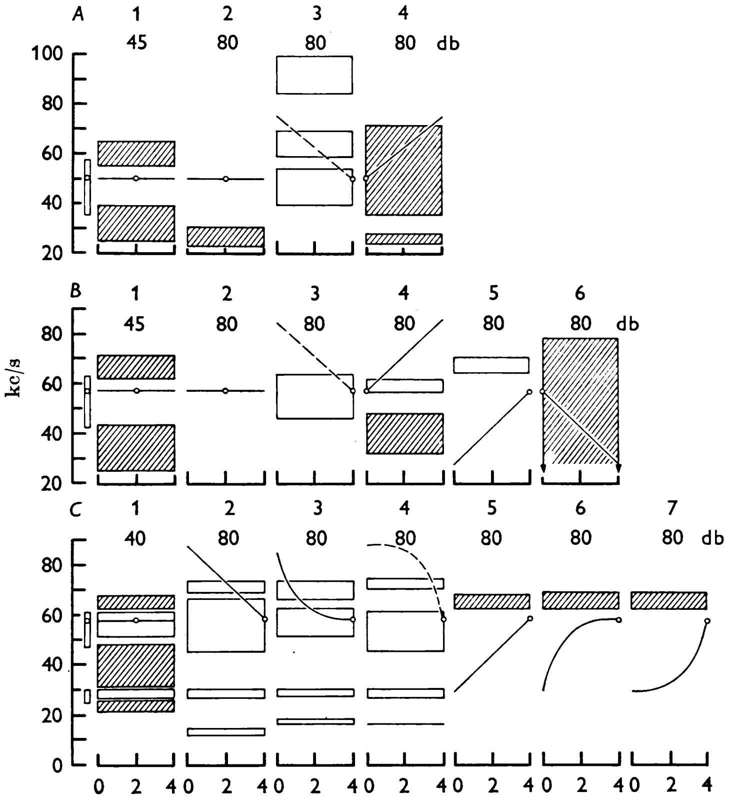

Fig. 9. Responses of three neurones (*A*, *B* and *C*) to complex sounds. All symbols have the same meaning as in Fig. 6, 1 and Fig. 8 (see text).

delivered with this FM tone pulse, the neurone showed responses if the frequency of tone pulse II was in one of the ranges indicated by the three open squares (*A* 3). The bottom square was to be expected because the sounds in it were, *per se*, excitatory ones for this neurone, but the other two squares were not. The neurone showed a response to the FM tone pulse sweeping from 50 to 75 kc/s. The response was, however, inhibited by pure tone pulses within the shaded squares (*A* 4). It was noticed that the sounds which caused responses in *A* 3 inhibited the response in *A* 4.

A neurone in Fig. 9*B* had similar ranges for excitation and inhibition to those in Fig. 9*A* as far as pure tone pulses were concerned (*B* 1 and *B* 2), but the ranges were different when certain A-FM tone pulses were used as tone pulse I (*B* 3–*B* 6).

Few data have been presented which may explain inhibitory ranges such as those shown in Fig. 9, *A* 4 and *B* 6. However, these data indicate that the range of FM tone pulses to which a neurone can respond is very much narrowed by the presence of other sounds.

In Fig. 9*C*, a neurone was excited by sounds in two ranges which were sandwiched in between inhibitory ranges (*C* 1). When tone pulses sweeping from 87 to 58 kc/s were delivered as tone pulse I, the responses to them were augmented by tone pulse II in four ranges as shown by the open squares in *C* 2 and *C* 3.

Responses to FM tone pulses sweeping from 29 to 58 kc/s in various functional forms were not retained when the sounds between 62 and 68–69 kc/s were delivered together with the FM tone pulses (*C* 5–*C* 7). It was noticed that some sounds inhibiting the response to the 40 db SPL sound at the best-frequency augmented the responses to the FM tone pulses. A necessary condition under which a neurone could respond to a certain sound in the presence of others was not simple for some asymmetrical, FM-insensitive and upper-threshold units when a combination of pure and FM tone pulses was used.

Responses of FM-sensitive neurones to complex sounds. FM-sensitive units had broad frequency ranges of sounds which inhibited responses to FM tone pulses (e.g. Fig. 3, *A* and *B*; Fig. 4, *B*; Fig. 6, *D* and *E*; Fig 10, *A*, *B*, and *C*; Fig. 11). In Fig. 10*A*, a neurone was activated by downward sweeping FM tone pulses (*A* 1 and *A* 3), but not by upward sweeping FMs (*A* 2 and *A* 4). Responses to the FM tone pulses sweeping downward were inhibited by sounds in shaded areas of *A* 1 and *A* 3, while summation or facilitation was observed when pure tone pulses in an open square were delivered with an FM tone pulse sweeping upward, although the neurone did not respond to either of them alone (*A* 4). In *B*, responses to FM tone pulses of 80 db SPL were suppressed to some extent by tone pulse II (B 1 and B 2). Clear inhibition by tone pulse II occurred on responses to FM tone pulses of 47 db SPL (B 3 and B 4). In *C*, an FM-sensitive unit had a small excitatory area around 50 kc/s. The minimum threshold was above 80 db SPL (*C* 1). Augmentation and/or inhibition of responses to FM tone pulses by pure tone pulses were observed as shown in *C* 1–3. In general, the inhibitory range of FM-sensitive unit included and extended below the sweep range of the FM pulses. Therefore, presence or absence of responses of FM-sensitive units strongly depended on what components existed together with an FM component in complex sound.

When one component in complex sound shows frequency sweep, others also show it, in general (Potter *et al.* 1966). Therefore, the effect of FM tone pulses on a response to a certain FM was also studied in several neurones. An FM-sensitive unit was sampled in such an experiment (Fig. 11). This unit was activated only by downward sweeping FM tone pulses (Fig. 11, 1 and 2). A minimum rate of frequency sweep, required to excite the neurone, was about 13 kc/s per 4 mseconds. The range in which tone pulse II (pure tone) inhibited responses to tone pulse I (FM) did not include the initial

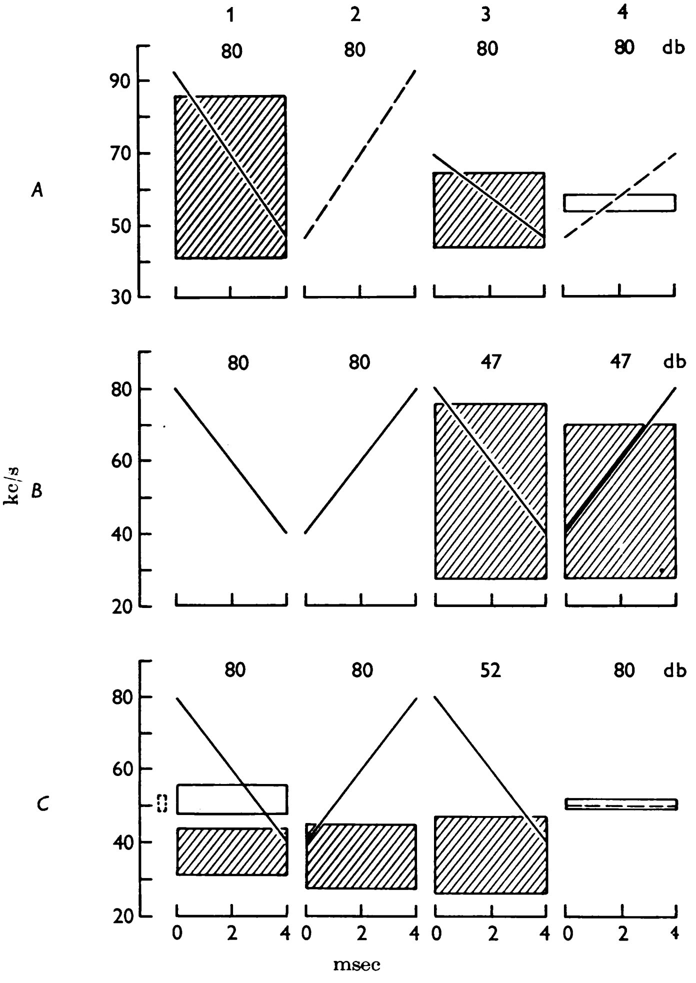

Fig. 10. Responses of three FM-sensitive units (*A*, *B*, and *C*) to complex sounds. All three neurones had no excitatory areas, but neurone *C* discharged an impulse for pure tone pulses of about 50 kc/s in a very low probability. All symbols have the same meaning as in Fig. 6, 1 and Fig. 8 (see text).

frequency of the FM tone pulse (3–5). When tone pulse II was FM pulse with a final frequency of 100 or 80 kc/s, certain FM tone pulses sweeping upward across the inhibitory area inhibited the response to tone pulse I (6 and 7). However, many tone pulse II sweeping toward 60 or 50 kc/s which were in the inhibitory range completely inhibited the response (8 and 9). Some inhibitory FM tone pulses in 9 were excitatory when they were delivered alone. This was also true in 10 and 11, where the terminal frequency of tone pulse II was 40 or 30 kc/s. That is, the neurone showed no response to simultaneous delivery of two excitatory FM tone pulses.

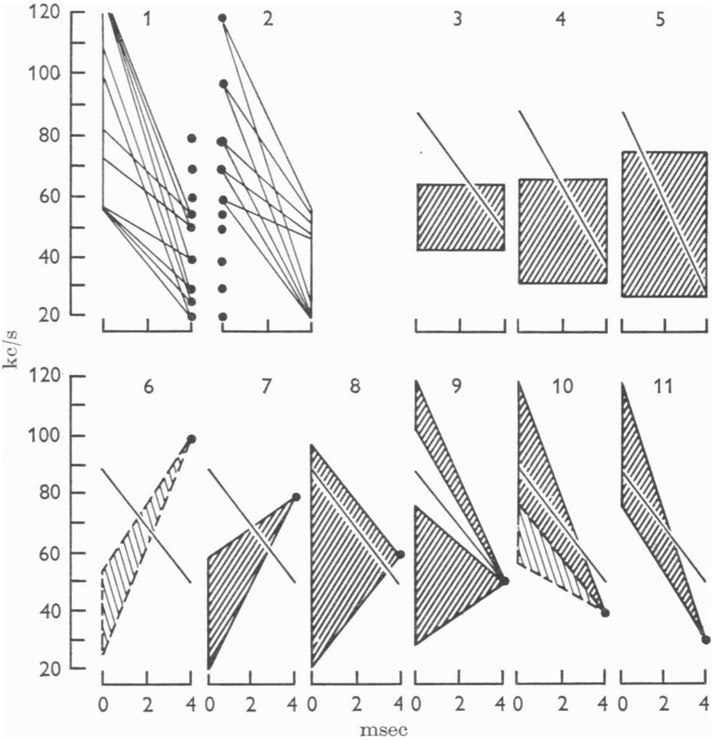

Fig. 11. Inhibitory ranges measured with pure and FM tone pulses for responses of an FM-sensitive unit with no excitatory area. 1 and 2: by delivering various A-FM tone pulses in which frequency sweep converged to (1) or diverged from each filled circle (2), the ranges of FM tone puses which excited the neurone were measured as shown by sectors. The neurone responded only to FM tone pulses sweeping downward. 3–5: widths at 80 db SPL of inhibitory areas in which tone pulse II (80 db SPL pure tone) inhibited the response to tone pulse I (80 db SPL FM). 6–11: ranges of tone pulse II (FM) which inhibited completely (heavily shaded sectors) or incompletely (faintly shaded ones) the response to tone pulse I (FM sweeping from 90 to 50 kc/s at 80 db SPL). The terminal frequency of tone pulse II is indicated by a filled circle (e.g. 100 kc/s in 6). All symbols have the same meaning as in Fig. 6, 1 and Fig. 8 (see text).

Some species of bats (e.g. rhinolophids and some hipposiderids) emit orientation sounds consisting of a long constant frequency portion and a short frequency modulated part at the end (e.g. Griffin, 1958; Pye, 1966). For these bats, the analysis of the FM part as well as the constant frequency part may be important. Therefore, the effect of pure tone pulses of 4 or 40 msec duration on responses of FM-sensitive units were studied by delivering pure tones before FM sounds without an intervening silent period. As shown in Fig. 6, *D* and *E*, Fig. 10, *A*, *B* and *C*, and Fig. 11, initial frequencies of downward sweeping FM tone pulses were not covered by inhibitory areas, but final frequencies were. When the frequency of the pure tone pulse was almost the same as the initial frequency of an FM, as in natural sound, the response to the FM tone pulse was not affected by the pure tone pulse irrespective of its duration. The response was, however, usually inhibited when the frequency of the pure tone pulse was within the inhibitory range. In Fig. 10*A*, when the initial frequency of tone pulse I was lowered, the uppermost frequency of the inhibitory sound became lower and the initial frequency was kept outside the inhibitory range. Figure 11 shows that the inhibitory range widened when the range of frequency sweep of tone pulse I was expanded toward lower frequencies. However, the initial frequency was always outside the inhibitory range, but the final frequencies were inside (3–5).

In the neural analysis of complex sound, a strong tendency was the restriction of conditions under which single neurones were activated, i.e. neurones at higher levels responded to a more restricted sequence or set of external tonal events than did those at lower levels.

DISCUSSION

In the present paper, properties of single neurones are described in relation to acoustic stimuli designed on the basis of some important parameters of human speech. There is, however, no intention of saying that the behaviour of the single neurones described here is directly concerned with the analysis of human speech. Single unit study with animals which cannot articulate human speech probably embodies limitations as a method of exploring the mechanism of the neural analysis of speech, because the importance of articulatory activity in the perception of speech rather than acoustic factors has been underlined in a few theories (Liberman, 1957; Fry, 1959). However, the principles illustrated in the bat seem to be broadly applicable to other mammals with suitable adjustment of the parameters of stimuli, since they are based on the notion of lateral inhibition which is a general mechanism having been psychologically and/or electrophysiologically demonstrated in different sensory systems of various animals (e.g. Békésy, 1967). The experiments performed with the bat may contribute to an understanding of the way complex sounds including human speech are analysed.

A human ear is most sensitive to sounds of about 3 kc/s in a free sound field (Licklider, 1951) while the sensitivity of the ears of a Yuma bat is greatest to sounds of 40–60 kc/s in terms of neural activity. Thus, all parameters of sound stimuli used in the present experiments may have to be expanded 10–20 times in the time dimension in order to have tonal stimuli suitable to human ears. The FM tone pulse sweeping one octave within 4 msec may be surmised to correspond to a transition sweeping one octave within 40–80 msec, which is commonly found in human speech.

Principles for responses of collicular neurones to FM and complex sounds in relation to some components in human speech. If we consider that tone pulse I, being a pure or FM tone pulse, represents a certain component in a complex sound (e.g. a formant or its transition in human speech), tone pulse II delivered simultaneously with tone pulse I may correspond to either higher or lower components according to its relation to tone pulse I.

Responding to complex sound, single neurones are, probably, most concerned with the components having frequencies identical to their best frequencies, except for FM-sensitive units. Hereafter, such components are called 'BF components'. Since tone pulse I usually was at the best frequency of a given neurone or FM sounds sweeping to or from the best frequency, it is a BF component or its frequency modulation (e.g. a certain formant or its transition).

The following principles can be said for several types of neurones in the inferior colliculus on the basis of the present experiments (refer to Fig. 12).

(*a*) A symmetrical unit responds to any FM (frequency modulation) of the BF component and the response is scarcely inhibited by other components in a complex sound.

(*b*) In an asymmetrical unit, the extent of FM of the BF component which can excite the neurone is limited by the inhibitory areas on one or both sides of an excitatory area. Inhibitory areas on the low frequency side tend to be larger than those on the high frequency side.

(*c*) The limitation is stronger for FM occurring toward the original frequency of the BF component than for FM starting from it.

(*d*) The response to the BF component is inhibited by lower and/or higher components unless these are outside the inhibitory areas. Neurones sensitive only to downward sweeping FM tone pulses were more often sampled than those sensitive only to upward sweeping FMs (Suga, 1965*c*). In the present sample, the neurones which had inhibitory areas only at frequencies higher than their excitatory areas were rarely found. These data indicate that, (*e*) in many asymmetrical units, lower components are more important than higher ones in determining whether response occurs to the BF component.

(*f*) In an FM-insensitive unit, inhibitory areas on both sides of an excitatory area limit the extent of FM of the BF component which can activate the neurone. Especially, responses to FM toward the best frequency are strongly restricted by these inhibitory areas. (*g*) When lower and/or higher components are within the inhibitory area or areas, the response to the BF component is inhibited. Therefore, this type of neurone responds to more restricted combinations of components than does the asymmetrical unit.

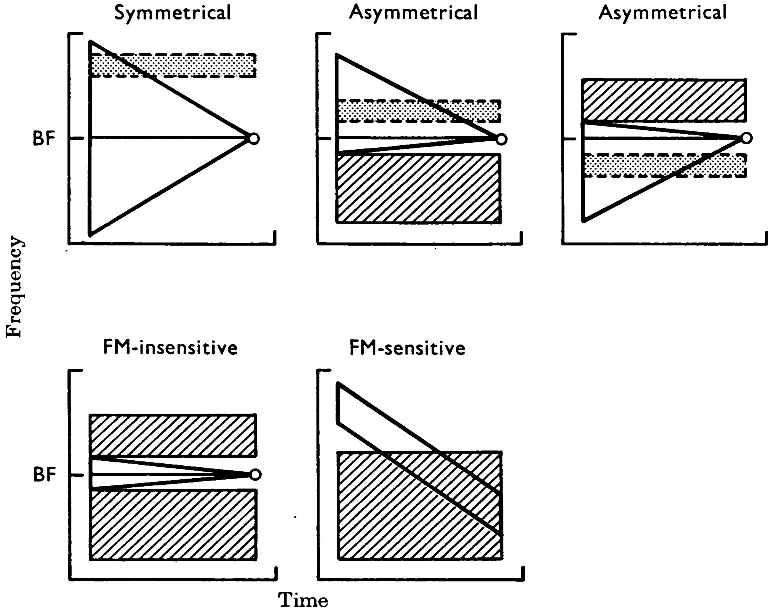

Fig. 12. The schematic presentation of characteristics of four types of inferior collicular units in terms of responses to FM and complex sounds. The ordinates and abscissas represent frequency and time, respectively. BF means the best frequency of a given neurone. The BF component is shown by a horizontal line with an open circle at its right end. Each neurone responds to FM of the BF component when it occurs to terminate at the best frequency within the open triangles. The responses are, however, completely (or partially) inhibited by other components when these are in the shaded (or dotted) squares.

(*h*) An FM-sensitive (or FM-specialized) unit with either no or very small excitatory area responds selectively to FM of a certain component. The direction, range, rate and functional form of a frequency sweep are especially important in activating this type of neurone. (*i*) The response is, however, inhibited by another component in a range so wide that it involves even frequencies in the FM of a certain component which excites the neurone. Thus, the condition necessary to excite the FM-sensitive unit depends not only on the characteristics of the frequency modulation, but also other components.

(*j*) The fact that the initial frequency of the downward sweeping FM tone pulse was kept outside the inhibitory range is important for deciding whether FM-sensitive units respond to FM components in complex sounds. When two phonemes are combined as in a monosyllable, some component in the phonemes may show transition, that is, an FM component may appear. In such a monosyllable, the preceding phoneme usually includes frequencies similar to the initial frequency of the FM component. Therefore, if the initial frequency of the FM component which excited an FM-sensitive unit were in an inhibitory area, the neurone would not respond to the FM component in the monosyllable. In the present experiments, FM-sensitive units were not sampled which responded only to upward sweeping FM tone pulses, the initial frequencies of which were outside an inhibitory range.

(*k*) An upper-threshold unit does not respond to the BF component and/or its FM when its intensity is stronger than upper threshold. The response of the neurone is inhibited by other strong components in a certain range. Some upper-threshold units also have asymmetrical or FM-insensitive or FM-sensitive characteristics. Such units are not only specialized for the analysis of sound structure in frequency but also in intensity. It is to be expected that the upper-threshold units respond to a sound changing from low intensity to high, but not to a sound changing from high intensity to low.

Structural requirement of single neurones for complex sound. At the inferior colliculus, the analysis of complex sounds is not performed in such a way that single neurones with narrow excitatory areas always respond when certain components of complex sound fall into the excitatory areas. Many neurones require a certain structure in the complex sound in order to be excited by it. That is, neurones except for symmetrical ones are essentially activated by single components of the complex sound, but only when the sound has no components in the inhibitory areas.

Another system may be proposed for the neural analysis of complex sound, in which single neurones do not respond to any single components of the complex sound, but to particular combinations of two or more components, as the result of summation or facilitation. In the present experiments, neurones with this type of requirement were not found. This may be simply due to the fact that the probability of activating such neurones by delivering the appropriate combination of sounds is low.

Sounds used by bats. For echo-location, a variety of sounds is used by different species of bats (e.g. Griffin, 1958; Novick, 1963; Pye, 1966). These are pure or FM tone pulses or combinations of these two or click sounds. The neurones found in the inferior colliculus could serve to analyse these sounds.

In bats, orientation sounds have received most of the attention of behavioural scientists because of echo-location. Invading a roosting place of many bats, such as a cave or attic, one may often hear a chattering noise of high frequency. It is to be expected that bats acoustically specialized for echo-location use sounds as the most effective means for communication, but this question has not been studied. Sounds for communication may have a structure differing from that of orientation sounds in frequency and temporal pattern. The complex properties of collicular neurones may represent function in communication and not only in echo-location.

Amplitude-modulation (AM) included in the FM tone pulses used in the present experiments. The frequency–response curves of the condenser loudspeakers used in this experiment were not flat as shown by dotted lines in Figs. 3 and 4 in spite of the constant input voltage to the loudspeakers, so that FM tone pulses were always amplitude-modulated in addition to the 0·5 msec rising and decaying phases of tone pulses. The effect of the AM on single neurones may, however, be neglected when differences among neurones were studied because the AM was approximately constant in the different FM tone pulses.

Acoustic psychology shows that FM tone pulses have the effect of AM on hearing even if a loudspeaker has an uniform output for all frequencies, because equal-loudness curves are a function of both the frequency and intensity of sound (Fletcher & Munson, 1933) and pitch depends not only on frequency but also intensity except for sounds of 1–3 kc/s (Stevens, 1935). Therefore, it may be asked whether single neurones respond to FM or change in loudness. In order to eliminate the factor of AM in terms of psycho-acoustics and to study only the effect of FM on hearing, FM sound would have to be modulated in amplitude to be parallel to the equal-loudness curves, which may be different from specimen to specimen (G. von Békésy, personal communication). However, no experiments have been performed yet with this viewpoint. It is not clear how the activity of single neurones with no or narrow excitatory areas and showing phasic on-responses relates to the psychological event, loudness.

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