

Responses of Auditory Neurons in the Forebrain of a Songbird to Stimulation with Species-specific Sounds*

Hans Joachim Leppelsack and Monika Vogt

Lehrstuhl für Allgemeine Zoologie, Ruhr-Universität Bochum,
Postfach 2148, D-4630 Bochum-Querenburg, Federal Republic of Germany

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Summary. 1. Auditory stimuli consisting of tape-recorded natural sounds were used in a study of 129 neurons in Field L of the caudal neostriatum in the forebrain of curarized starlings (*Sturnus vulgaris*).

2. An extensive program of stimuli comprising many different signals (109 sound elements) was devised in order to permit identification of even very highly specialized neurons.

3. As a rule, the time courses of the neuronal responses parallel those of certain parameters or parameter combinations of the sound stimuli. The responses of a few very specialized neurons, however, did not reflect any distinguishable temporal substructure within the effective sounds.

4. 64 neurons were examined with respect to the number of stimuli, out of a sample of 80 sound elements, eliciting a response. 24 of these neurons responded to less than 10 of the 80 natural sounds. These include neurons responding only to a single sound or to sounds of a single type.

5. 30 of the 64 neurons responded most strongly, or exclusively, to sounds of a single type.

6. The criterion determining whether a neuron responds to a given sound may be a single parameter, a combination of parameters, or the entire complex of parameters describing the sound.

I. Introduction

A number of studies have been made of the responses of neurons in the auditory centers of the bird forebrain to stimulation with artificial sounds (Biederman-Thorson, 1970; Leppelsack and Schwartzkopff, 1972; Leppelsack, 1974a, b). Worden and Galambos (1972) emphasized the possibility that auditory systems have evolved special mechanisms for the recognition and processing of biolog-

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ically meaningful sounds, which are not called into play by simple artificial sound stimuli. "Feature detectors", for example, and neurons involved in the identification of specific sounds may not be revealed by experiments using only simple artificial sounds as stimuli.

In view of this possibility, Winter and Funckenstein (1970), Wollberg and Newman (1972), Newman and Wollberg (1973a, b), and Winter and Funckenstein (1973) studied mammalian cortical auditory neurons, using species-specific sound stimuli. This paper describes related experiments with birds. A survey of the response capabilities of the neurons has been made, with the greatest possible variety of species-specific stimuli.

The starling was chosen as the object of study, for it has an extensive repertoire of songs and, as a social animal, uses a number of different sounds for intraspecific communication.

II. Materials and Methods

Experiments were done on 43 starlings (*Sturnus vulgaris* L.). All the data to be presented were obtained from neurons in Field L of the caudal neostriatum, in the left hemisphere of the forebrain. The electrodes were glass capillaries filled with 3 M NaCl. During the experiments the animals were curarized. A more detailed description of the experimental conditions has been published elsewhere (Leppelsack, 1974a).

The stimuli consisted predominantly of recordings of natural sounds, the calls and songs used by starlings in communication. These were recorded on magnetic tape (Nagra IV-L) with a half-inch Brüel and Kjaer condenser microphone. Eleven passages selected from the recordings were played back on a Revox tape recorder. The sequence of eleven passages, each separated from the next by a pause of at least 1.5 s, had an overall duration of 77 s. The amplitudes and frequency spectra of the different sounds in the series were determined from oscillograms and sonagrams (Fig. 1). Temporally distinct subunits of the sounds (cf. Fig. 1c and d), and the sounds with no clear temporal subdivisions, are designated "sound elements". The stimulus program was made up of 109 such sound elements.

The significance of such sounds in communication has been analyzed (Hartby, 1969; Bahrig, personal communication; Schneider, 1960). The sounds upon which the stimulus program was based occurred in one or more variations; these basic sounds will now be described.

The calls and songs of starlings differ considerably in their frequency content. Some have a nearly sinusoidal waveform (e.g., Fig. 1a), others comprise a narrow frequency band (e.g., the aggression sound in Fig. 1b), and still others are broad-band "noisy" sounds with components extending over the entire range of frequencies the starling produces (e.g., the "self-assertion" sound of Fig. 1c). In addition to these various frequency compositions, some of the sounds display frequency modulation at different rates and of varying duration; an example of such modulation is found in the "pacification" sound of Figure 1d, the whistle introducing a song (Fig. 1f), and the song element shown in Figure 1k. Other sounds shown in Figure 1 include the nestling call of a young starling (Fig. 1h), a fear squeal (Fig. 1i), a threat call (Fig. 1e), a special call that has been learned among a particular group of starlings (Fig. 1g), a copulation call of the male, at a frequency of 8 kHz (Fig. 1j), and part of the starling's song (Fig. 1l). In addition to these sounds the stimulus program also included non-vocal sounds such as the beating of wings and the striking of the beak against a branch.

This stimulus program was played through several times while the activity of a neuron was being recorded—three times as a rule, and at most nine times. In addition, sections of the program lasting about 3 s were selected and used as stimuli 14 times in immediate succession.

The responses of the neurons were recorded on magnetic tape and later photographed or analyzed by computer (PDP-12, Digital Equipment Corp.), so that either the individual responses, a summary of the responses, or a peri-stimulus-time histogram (cf. Fig. 2) could be studied. When the 3-second sections were used as stimuli, PST histograms of the responses were compiled (Fig. 2).

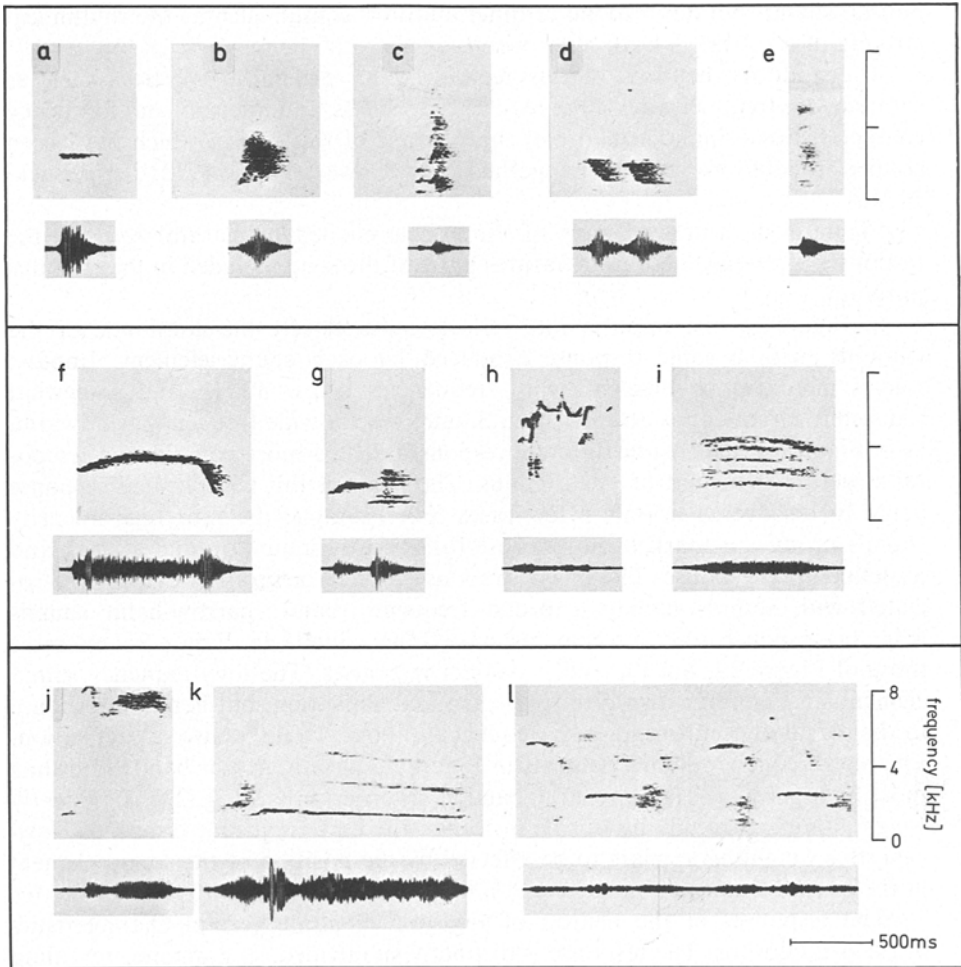


Fig. 1a-j. Oscillograms (lower records) and sonograms (upper records) of the basic starling sounds used in the stimulus sequence. **a-c** sounds illustrating the range of frequency bandwidths. **d, f, h, k** sounds varying in frequency modulation. Sounds **a, k** and **l** are taken from the song, while the remaining sounds have a more special significance as follows: **b** aggression sound; **c** self-assertion sound; **d** pacification sound; **e** threat call; **f** whistle introducing the song; **g** learned sound; **h** nestling sound; **i** fear squeal; **j** copulation sound of the male

III. Results

A. Characteristics of the Auditory Neurons of the Forebrain

Data were obtained from 129 Field-L neurons. Each of these responded to at least one species-specific sound in the sequence of natural sounds. A large but not precisely determined number of neurons in this region do not respond to these natural sounds, nor do they respond to the artificial sounds presented. Two neurons have been recorded which failed to respond to species-specific

natural sounds but did respond to other auditory stimuli such as the rhythmical striking of a starling's beak upon wood.

The auditory neurons in this region exhibit general properties—such as spontaneous frequency, response to artificial sounds, and intensity and frequency characteristics—similar to those of the neurons of this region which have been studied in detail previously (Leppelsack and Schwartzkopff, 1972; Leppelsack, 1974a).

Figure 2 shows an example of the effects elicited by natural sounds: the responses of a single neuron to various parts of the song included in the stimulus program.

In Figure 2a, the impulse rate reflects quite closely the amplitude of the stimulus, with a tonic response produced by each sound element. Impulse rate is increased by elements with frequencies below 3 kHz, and somewhat reduced for frequencies above 4 kHz. Sounds with a wide frequency bandwidth, as in Figure 2b, elicit quite different responses, with a more complicated temporal structure than that of the stimulus. The basis of this complicated response could be discovered in only a few cases. For example, the four high-intensity sounds produce a marked on-response followed by inhibition and a weak and ill-defined off-response. The phasic response of such neurons is evidently associated with sounds having a broad frequency band; narrow-band sounds (Fig. 2a) produce only a tonic response. The sounds in Figure 2c resemble those of Figure 2a, but they elicit distinct responses. The low-frequency sound elements in Figure 2c also give rise to marked activation, but here the response to the elements comprising only frequencies above 4 kHz is also an activation. The high-frequency sound elements in Figure 2c have a greater bandwidth than those in Figure 2a. Thus the large-bandwidth criterion (cf. Fig. 2b) is evidently weighted more strongly by this neuron than the high-frequency criterion. However, this weighting appears to be affected by the position of the sound element in the overall frequency range.

The responses of the neuron of Figure 2 illustrate certain characteristics of Field-L neurons. The response is distinctly subdivided, in a manner revealing a complex dependence upon combinations of parameters; regular repetition of the same stimulus gives relatively uniform responses. Only in certain neurons does a sound elicit a “categorical” response, regardless of the detailed parameter combinations. Another typical attribute is the rarity of inhibition in a response; the responses to artificial sounds, by contrast, represent inhibition in about 47% of all cases. A peculiarity of this neuron is the relatively high spontaneous discharge (18.5 imp/s) and the large number of sounds to which it responds. On the other hand, it is typical that these two properties occur together, when they occur at all; conversely, a low rate of spontaneous activity is associated with an ability to respond to only a small number of sounds.

B. Degree of Selectivity and Its Distribution in the Sample of Single Neurons

In contrast to neurons like that of Figure 2, which give responses reflecting in detail the parameters of certain sounds, other neurons respond to a limited number of sounds, in some cases to only one of the 109 sound elements presented.

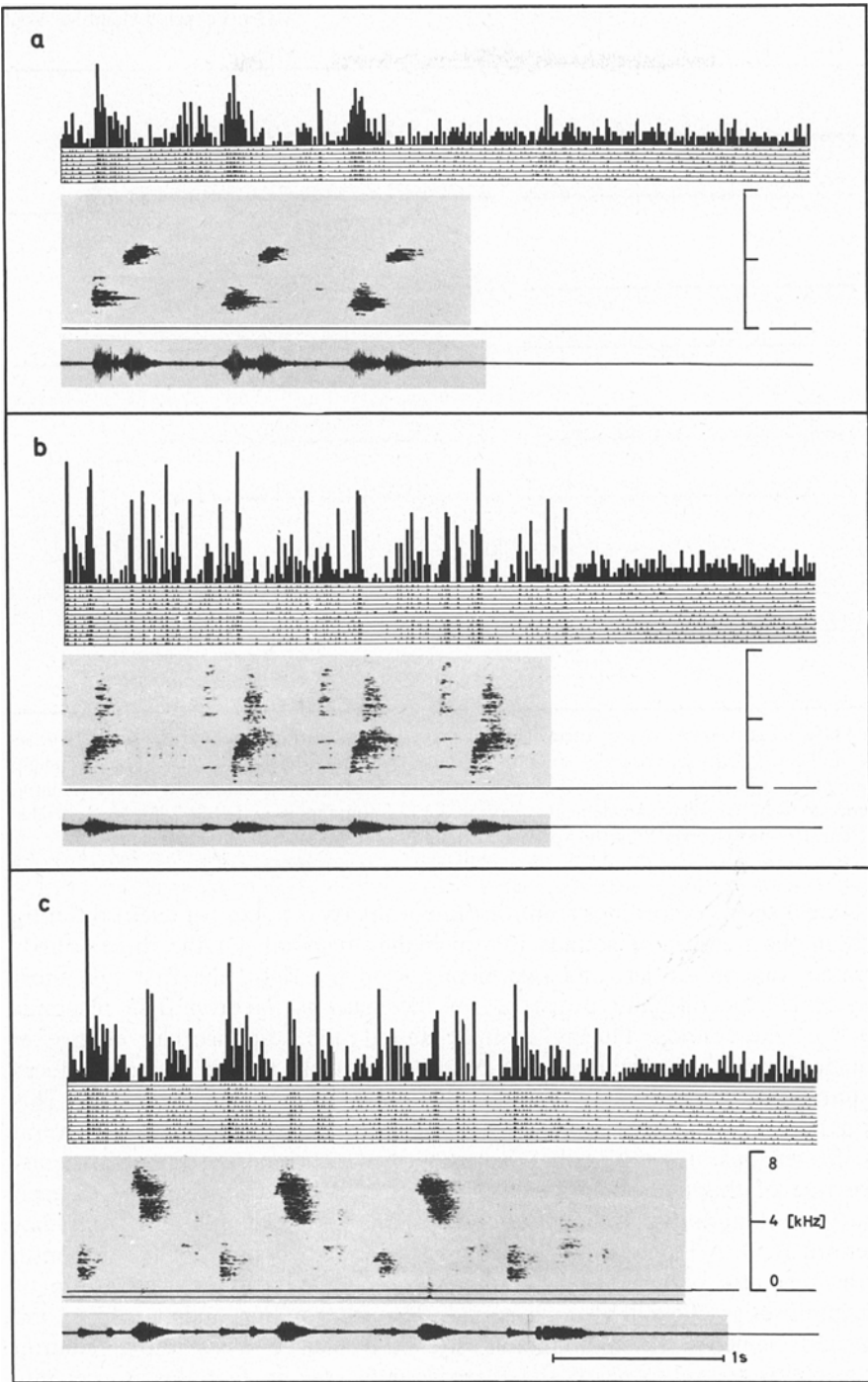


Fig. 2a–c. Responses of a single neuron (C 90) to different sections of the starling song (a–c). In each case the bottom record is an oscillogram of the sound stimulus, with the sonogram of the sound displayed above it. The response is represented by the sequence of impulses during 8 (a) or 14 (b and c) stimulus presentations, and above these records the PST-histogram obtained from them

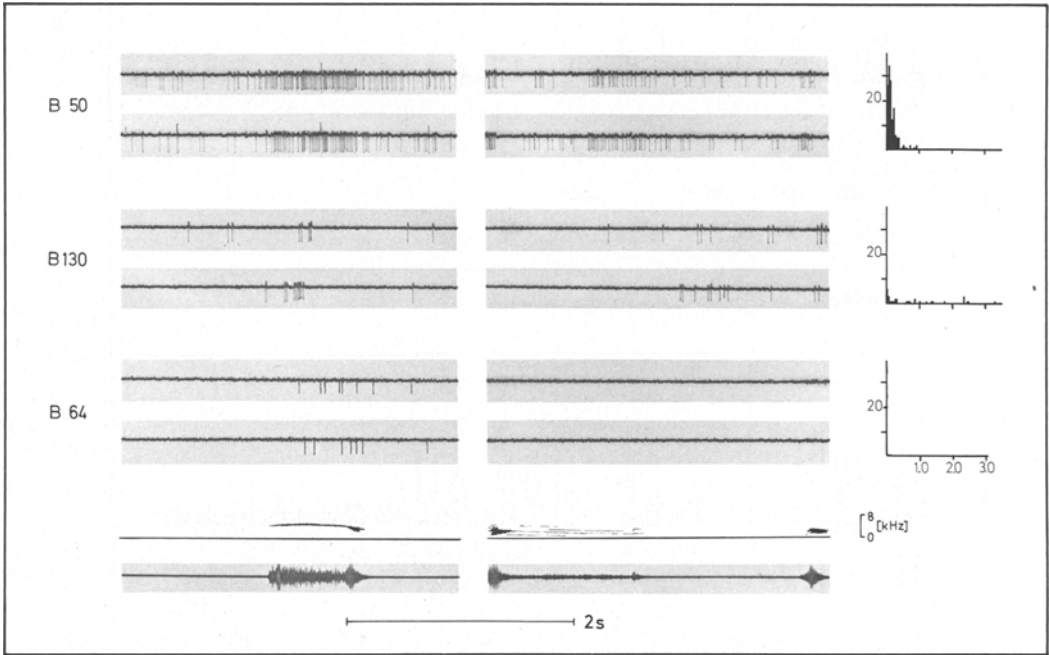


Fig. 3. Differences in selectivity of three neurons responsive to natural sounds; the interval histograms of the right characterize the spontaneous activity of these neurons. 109 sound elements were presented in each case. Neuron B 50, with an average spontaneous discharge rate of 5.6 imp/s responded to 94 of the 109 sound elements; Neuron B 130 (spontaneous activity 1.2 imp/s) responded to 47 elements, and Neuron B 64 (no spontaneous activity) responded to only 1 element

Figure 3 shows recordings from three neurons (two traces for each) differing greatly in the number of sounds to which they respond. Of the three sounds illustrated, one on the left and two elements on the right, the first two most clearly reveal the different properties of the neurons. Neuron B 50 responds to each of the sounds. During a single sound, the response can change in character; for example, the frequency modulation in the second sound produces first activation, then absence of response, and finally strong activation. This neuron responds to 94 of the 109 sound elements presented, and in several cases the response resembles that just described. The mean spontaneous discharge rate of this neuron is 5.6 imp/s. Neuron B 130 also responds to each of the three sounds illustrated, but the response is quite different from that of Neuron B 50. A longer time elapses prior to the appearance of the response, and the response pattern itself is not so complicated; rather, one group of nerve impulses is elicited by each sound. This neuron responds to 47 of the 109 sound elements. Its spontaneous rate of discharge is 1.2 imp/s. Neuron B 64 responds to only one of the three sounds, and in fact this is the only one of all the 109 sounds to which it responds. This neuron is not spontaneously active.

For each of 64 neurons tested several times with the full stimulus sequence described above, all of which respond to one or more sounds in this sequence,

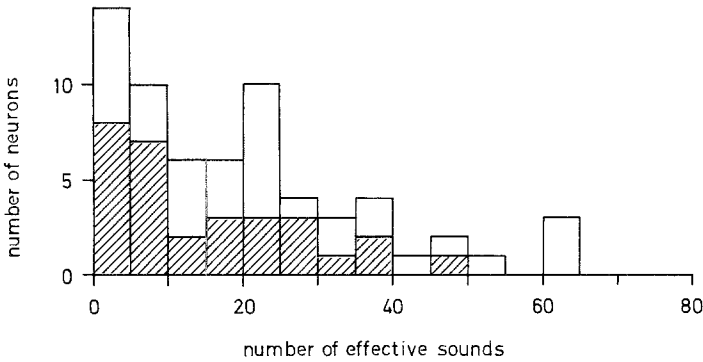


Fig. 4. Distribution of degree of selectivity in a sample of 64 neurons. Of 80 stimulus sounds, each neuron responded to a certain number and failed to respond to the rest. In the diagram, the neurons are grouped into bins according to the number of effective sound stimuli; e.g., 14 neurons responded to only 1–5 sounds (leftmost column) and 3 neurons responded to 61–65 sounds (rightmost column). Of the neurons in each bin, those represented by the cross-hatched part of the column responded preferentially to a single type of sound (or single sound); in the remaining cases, the effective sounds were of various types

the number of effective sound elements is counted. This count includes 80 distinct sound elements—those which are so clearly separated in time that there is no doubt which element has elicited the response. The neurons are divided into classes according to the number of sound elements to which they respond (i.e., 1–5 elements, 6–10 elements, and so on), so that the data can be summarized in a plot reflecting the distribution of the “degree of selectivity” in the population of cells (Fig. 4). “Specialist” cells are at the left of the plot, and “generalists” toward the right. The lowest degree of selectivity is represented by the few single neurons responding to 61–65 of the 80 elements presented. Most are much more selective in their responses. More than one-third (24 of 64) of these cells respond to fewer than 10 of the 80 sound elements.

The neurons can be further subdivided into two groups, based on the degree of similarity of the sounds to which each responds. Those in one group (represented by the cross-hatched portions of the bars in Fig. 4) respond “preferentially”—i.e., either exclusively or more strongly—to sounds of a single type. Even the sounds to which these neurons give weaker responses are similar acoustically to the preferred type. Accordingly, the number of sounds to which each neuron in this group responds tends to be small. The other group (white portions of the bars) consists of neurons with equally strong responses to sounds of several different types.

C. Form of the Response and Criteria for the Occurrence of a Response in a Given Neuron

The example of Neuron C 90, in Figure 2, illustrates that the responses of a single forebrain neuron to different sounds can differ depending upon the nature of the sound stimulus. This suggests the complementary comparison—that

is, of the responses of different neurons in the region studied to the same sound. Figure 5 shows the responses of a number of different neurons to three different sounds. This figure is of course simply an example. In evaluating the responses and response criteria of the cells, all 109 sound elements were taken into account; as a rule more than the two responses shown in Figure 5 for each stimulus were recorded.

Figure 5a shows responses of 6 neurons to a starling whistle consisting of two elements, the first of which is low in intensity and frequency (1.7 kHz). The second element is louder, with frequency near 2.5 kHz. The frequency bandwidth of this element pair is very narrow and there is little modulation, whereas the intensity is strongly modulated. There are distinct differences in the intensity and time course of the six sets of responses. The three neurons represented in the upper traces give an on-response to the first element, and do not respond to the second element. In the cells of the lower traces the on-response is absent, and two of them (B 137 and B 40) respond to the second sound element.

Figure 5b illustrates the responses of 6 neurons to a two-part sound with a broad frequency spectrum. The time of onset of the responses varies widely, some cells responding shortly after the beginning of the sound and others giving only off-responses.

The sound used as stimulus in Figure 5c includes a complicated pattern of frequencies and intensities. To the human ear it is a long whistle falling slowly in pitch followed by a short whistle at a high, constant frequency. The stimulus may be described more precisely as comprising two noisy components with relatively broad frequency bands, two sine-wave sections at constant frequency, and a main section in which the fundamental frequency declines slowly and several higher harmonics are present.

It is interesting that the responses shown are clearly associated with the above mentioned components in the stimulus. For example, Neuron B 93a responds only to the noisy components, Neuron B 130 responds only to the first noisy component and to the frequency-modulated component over a small range, and Neuron B 37 responds only to the first noisy component and the first sine-wave component. The other cells respond to various combinations. It should be noted that Neuron B 50 is inhibited by both sine-wave components, whereas both noise and frequency modulation activate the neuron.

Comparison of these records shows that the neurons studied do not, as a rule, respond to a sound as a single entity; the patterns of their responses are clearly correlated with specific acoustical parameters or parameter combinations. These parameters, then, must represent the criteria determining the responses of the neurons. That the criteria of individual neurons differ is evident in the diversity of the responses to a given natural sound (Fig. 5). Examination of the sounds producing responses, to determine their common features and their differences from ineffective sounds, can reveal some of these criteria. For example, Neuron B 92 in Figure 5a responds to frequencies around 1.7 kHz but not 2.5 kHz. The responses of this neuron to other sounds confirm that the requirement for response of the neuron is a low frequency, about 1–2 kHz, whereas higher frequencies are not effective. As another example, Neuron B 93a

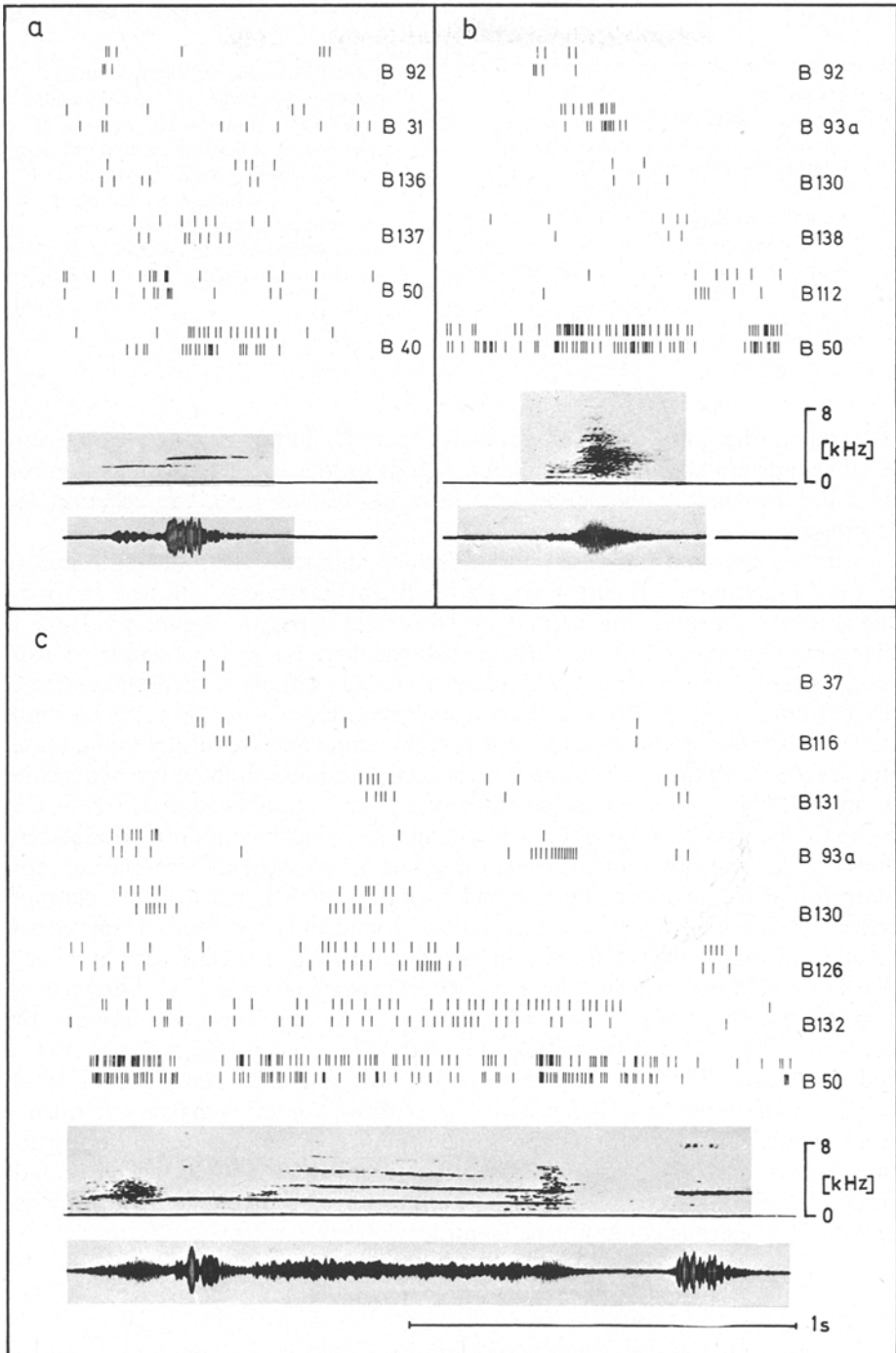


Fig. 5a-c. Responses of different neurons to a given sound. Three sounds are shown: **a** with a very narrow frequency band (sinusoidal waveform), **b** with a broad frequency spectrum, and **c** with a complex variation in time of the frequency and intensity parameters. For each neuron, the first two responses to the given sound recorded during a 77-s stimulus-sequence presentation are shown. The stimuli are represented by both oscillogram and sonagram

19	Frequency
4	Frequency modulation
5	Frequency bandwidth: extremely narrow
6	Frequency bandwidth: narrow
7	Frequency bandwidth: wide
3	Multiple frequency bands
6	Fear Squeal (Fig. 1i)
3	Whistle preceding song (Fig. 1f)
2	Nestling call (Fig. 1h)
9	Criterion unclear

Table 1. The nine identifiable criteria determining whether the neurons studied respond to a stimulus. The response of each neuron is determined predominantly by one of these criteria. The number of neurons, in a sample of 64 neurons responsive to species-specific sounds, characterized by each criterion is shown in the left-hand column

responds to the noisy sound elements in Figure 5b and c; neither very-narrow-band sounds nor frequency-modulated sounds produce a response. This neuron does not respond to the sound in Figure 5a. In this case, the criterion for response is evidently a large bandwidth.

Further neuronal response criteria become apparent when all the responses of the 64 neurons of Figure 4 are analyzed. In that figure, the neurons were categorized as responding to one or to several types of sound. In Table 1, the response criteria of the neurons are shown; these range from simple acoustical parameters to complete sound elements. As an example of the latter extreme, the nestling call (Fig. 1h) and the whistle preceding a song (Fig. 1f) are both relatively simple sounds having narrow bandwidths and frequency modulation. But neurons with these sounds as criteria do not respond to the same frequencies or modulation, presented in isolation or as part of other sounds. Only if a stimulus incorporates these parameters in the typical temporal arrangement does it elicit a response of these neurons. The simple acoustic criteria are most often found for neurons that respond to many sounds, whereas the complex criteria exemplified by the nestling call are found only for neurons specialized to respond exclusively to these sounds. In addition to the cells with extremely simple or complex criteria, there are neurons having criteria of intermediate complexity which can be termed "features". Among these features are the occurrence of several distinct frequency bands (e.g., in the fear squeal, Fig. 1i, and the whistle, Fig. 1f), frequency modulation, and a certain value of bandwidth. In the latter case the response is selective for every narrow frequency bands (sinusoidal waveform) for narrow bands, at frequencies differing for the various cells. By contrast, 19 neurons respond to sounds which include certain frequencies, regardless of the bandwidth of the sounds. The response criteria of 9 neurons could not be identified.

IV. Discussion

These studies have shown that the neurons of Field L differ greatly in degree of selectivity. Some neurons are functionally equivalent to a simple parameter filter. These include primarily neurons which act as frequency filters, in accordance with their threshold-vs.-frequency characteristic. This category also in-

cludes neurons responding preferentially to certain lateral position of the sound source or having a response phase-locked to the stimulus (Leppelsack, 1974a).

Other neurons respond to parameter combinations—for example, to the particular frequency mixture of which a sound is composed. In such cases both bandwidth and the position of the individual frequency bands determine the response. Neither single frequencies nor frequency bands uniformly distributed over the entire auditory range elicit responses of the neurons. Many of them respond only to very complex combinations of parameters, and the potential diversity of these is difficult to encompass experimentally. These neurons can usefully be designated “feature detectors”. In addition to these, there are neurons that respond to only one of the tested sounds, or only to sounds of a single type. That is, their responses are based on the totality of parameters comprising the sound, and not on distinguishable subsets of parameters (cf. Fig. 6, Neuron B 65). Simple artificial sounds elicit no response; the standard threshold curves can of course not be obtained for such neurons.

Neurons in this last category clearly appear capable of identifying specific sounds. What is not clear, however, is the role they play in the general neural recognition process.

The function of Field L in the overall auditory pathway is not yet clear, in view of the variety of responses observed there. In fact, there remains a fundamental doubt whether it will be possible to assign it a distinct and clearly defined function—such as, for example, the analysis of species-specific communication sounds, the recognition of individual species-specifics, or the like. Nor does comparison with published data on the midbrain of gallinaceous birds (Scheich, Koch and Langner, 1974) shed any direct light on the problem.

Comparison of the results presented here with the relevant work on the primate cortex published by Winter and Funckenstein (1970), Wollberg and Newman (1972), Newman and Wollberg (1973a, b), and Winter and Funckenstein (1973) is also difficult, since there is some contradiction between the findings of Newman and Wollberg and those of Winter and Funckenstein, especially in the area of neuronal specialization. However, there appear to be no fundamental differences between the forebrain auditory neurons of mammals and birds with respect to the processing of natural sounds—a basic similarity previously documented by comparison of their responses to artificial sounds (Goldstein, Hall and Butterfield, 1968; Hall and Goldstein, 1968; Leppelsack, 1974a).

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