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The Coding of Sound Signals in the Ventral-Cord Auditory System of the Migratory Locust, *Locusta migratoria* *

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Summary. Coding of auditory signals in the entire ventral-cord pathway of the migratory locust, *Locusta migratoria,* has been studied by extracellular recording of the responses of ascending neurons.

In order to exclude errors due to variation in the responses of neurons of a given type among different individuals, an effort was made to record successively from the greatest possible number of single cells at each station in each animal. Neurons of one type tested in different animals gave very similar responses; this suggests that there is also little interindividual variation among neurons of other types. Thus the various neurons of these animals can be compared for analysis.

Apart from the responses to the standard artificial sound (white noise, 20 ms duration, 2/s repetition rate), responses to simulated conspecific songs received the greatest attention.

The coding of individual parameters is described, with the intensity of artificial sound stimuli as an example. Taken together, all the neuronal responses in an animal permit discrimination of white noise bursts differing in intensity by as little as 10 dB.

Responses to the conspecific song and simulations of it are often not directly comparable with those to simple white-noise bursts. The temporal structure of the conspecific song has a considerable effect on neuronal response. All the important temporal parameters – syllable duration, syllable rate, verse duration, verse rate – are reflected in the overall neuronal response. Thus all this information is available for further analysis in higher centers.

Introduction

The responses of the auditory neurons ascending through the ventral cord to the supraesophageal ganglion of *Locusta migratoria* have been examined in great detail. Artificial sounds have been used to determine the way in which the parameters frequency, intensity, direction, duration and repetition rate are encoded in the responses of single neurons. Their response patterns permit the assignment of these neurons to different types (Kalmring, 1975 I; see Table 1).

In these earlier studies only one or a few neurons per animal were investigated. It could be, however, that neurons of the same type in different animals might in some cases differ considerably in magnitude (impulses per stimulus) or threshold of response. Differences in response magnitude can often be taken for differences in pattern, so that neurons in different animals can be assigned to a particular type only if a great many combinations of stimulus parameters are tested. Because of these differences, it has not previously been possible to derive an estimate of the overall coding performance of the auditory system in the ventral cord by comparing the responses of the known auditory neurons at this level. The experiments described here represent an attempt to make such a comparison, by recording from as many single neurons as possible in a single animal. The ventral-cord neurons ascending to the supraesophageal ganglion offer a number of advantages for such experiments. Their number is relatively small; in this part of the central nervous system the auditory system consists of about 15 neurons on either side of the cord. Most of these can be examined electrophysiolog-

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Table 1

Type	Response pattern	Preferred intensities/ frequencies	Responses to ipsi-/ contralateral stim.	Spont. activity	Habituation
B_1	tonic or phasic	low and intermediate intensities	ipsi > contra	low	yes
C_1	tonic	preferred answered intensity increases with frequency	ipsi > contra	relatively low	no
C_2			ipsi ≦ contra		
C_4			ipsi > contra	strong	
C_5		response magnitude increases with intensity at all frequencies	ipsi > contra	low	
C_7	weakly tonic		ipsi = contra	strong	
F_1	tonic; responses may outlast stimulus duration	reacting preferentially below 10 KHz	responding only to ipsilateral stimulation within an angle of 120°	no	yes
F_2		reacting only above 10 kHz		no	yes
G_1	phasic to weakly tonic		ipsi = contra	no	strong
K_2	tonic to 15 ms–20 ms stimulus duration	response magnitude increases with intensity at all frequencies	ipsi = contra	low	weak

ically with relative ease. They are third- and fourth-order neurons, so that the responses monitored result from a variety of synaptic events in which inputs from both tympanal organs are processed (Kalmring, 1975 I). These neurons evidently have an important "distributor" function in the central nervous system. The responses generated in the dendrite region are transmitted unaltered along the main branch of the axon to the supraesophageal ganglion (Kalmring et al., 1978).

As yet it has been impossible to be certain which cells in the auditory pathway are postsynaptic to these neurons, whether in the ventral cord or in the supraesophageal ganglion, though attempts have been made in locustids, tettigoniids and gryllids (Adam, 1969; Rheinlaender and Kalmring, 1973; Rheinlaender, 1975; Huber, 1977).

However, such experiments are hampered by the following factors. The responses of these neurons are transmitted, by way of numerous branchings in ventral cord and supraesophageal ganglion, to many—usually sensory—neuropile regions. At these branchings the responses can be considerably altered by a variety of time-dependent filter processes (Kalmring et al., 1978). In this situation it is impossible to predict exactly what information is transmitted to the postsynaptic cells. Moreover, the ventral-cord neurons ascending to the supraesophageal ganglion are multisensory information carriers; they also receive inputs from the vibration receptors on all six legs. It is likely that in the higher centers information about sound signals is processed along with other, non-tympanal acoustic sensory inputs (Bauer, 1977; Ernst et al., 1977; Boeckh et al., 1976; Waldow, 1975).

But we know that the sense of hearing is crucial in intraspecific communication and in detection of sounds in the environment; sound signals ought therefore to be unambiguously coded and detected in the central nervous system. Evidence that they are is provided by the results of various behavioral experiments (v. Helversen, 1972; Popov and Shuvalov, 1977; Huber, 1977; Elsner and Huber, 1973). The ascending neurons in the ventral cord may well play an important role in this regard.

In the experiments described here the responses of either 7 or 5 neurons of various types recorded successively at a single site on one side of an animal were compared; the stimuli were artificial sounds and simulated natural sounds. The latter were mainly based on white noise; the frequency spectrum of the conspecific songs is broad-band, and the neurons respond very similarly to conspecific songs and songs simulated by modulation of white noise (Kalmring, 1975 II). A sample of 7 neurons represents about half of all the known auditory neurons on one side of the ventral cord. Opportunities for comparison can be extended by recording from several animals and testing the neurons in different combinations each time. If recordings from neurons of a given type in different animals prove to show the same responses, it can be assumed that interindividual variation is also low in the remaining neurons. Once this is established, the way in which all the important auditory ventral-cord neurons participate in coding of sound signals in the ventral cord can be determined; a measure of the "total information" available at this level of the auditory pathway—the basis for all subsequent processing—is thus available.

Materials and Methods

The details of the experiments – animals, preparation, apparatus, procedure and data processing – have been described in Kalmring et al. (1978).

The responses of single neurons were recorded extracellularly with glass microcapillaries (filled with 3 M KCl or 3 M $CoCl_2$; resistance 8–20 MΩ). The reference electrode was a silver wire inserted into the abdomen. During the experiments the effort was made to record successively from as many neurons as possible in a single animal at the same station (from a circumesophageal connective at the entrance of the tritocerebrum).

As stimuli we used not only the artificial sounds described there, but also simulated natural sounds. The time course of amplitude of a double syllable of the conspecific song was simulated with a Complex Waveform Synthesizer (Exact, 202). This envelope curve was used to modulate tones of various frequencies and, in particular, white noise.

The syllable rate corresponded to that of the conspecific song (ca. 12/s); the verse rates used were 2/s, 1/s and 0.5/s. The verse rate of the conspecific song is about 1/s (Popov, 1969). Other parameters of the conspecific songs are described elsewhere (Kalmring, 1975 II).

Results

1. Responses to Artificial Sounds

The responses of seven different neurons recorded in succession from a single animal at the base of the tritocerebrum are shown in Fig. 1. For each sound are shown the individual responses to 10 successive identical stimuli; above these is the PST histogram calculated from these responses (Experiment No. LmF 19). The data are from one F_2 neuron (I), 5 different C neurons (II to VI) and one G_1 neuron (VII). F neurons give tonic responses often outlasting the stimulus. They are strongly direction-sensitive, responding only to sound presented ipsilaterally. They do not discharge spontaneously. C neurons always respond tonically and have a spontaneous discharge. The responses of G_1 neurons are phasic or weakly tonic, not directionally sensitive, and strongly habituating. These cells have no spontaneous discharge.

The responses of these 7 neurons to identical stimuli differ both in magnitude (impulses per stimulus) and latency (delay between onsets of stimulus and response) and in the distribution of the impulses in time. Certain neurons (Fig. 1: II, VI, VII) respond with remarkably fixed latency at suprathreshold intensities. Their discharge is also very regular, at least in the first part of the response, the instantaneous frequency often remaining nearly constant. Other neurons (Fig. 1: I and IV in particular) show more variance; the latencies of the individual responses

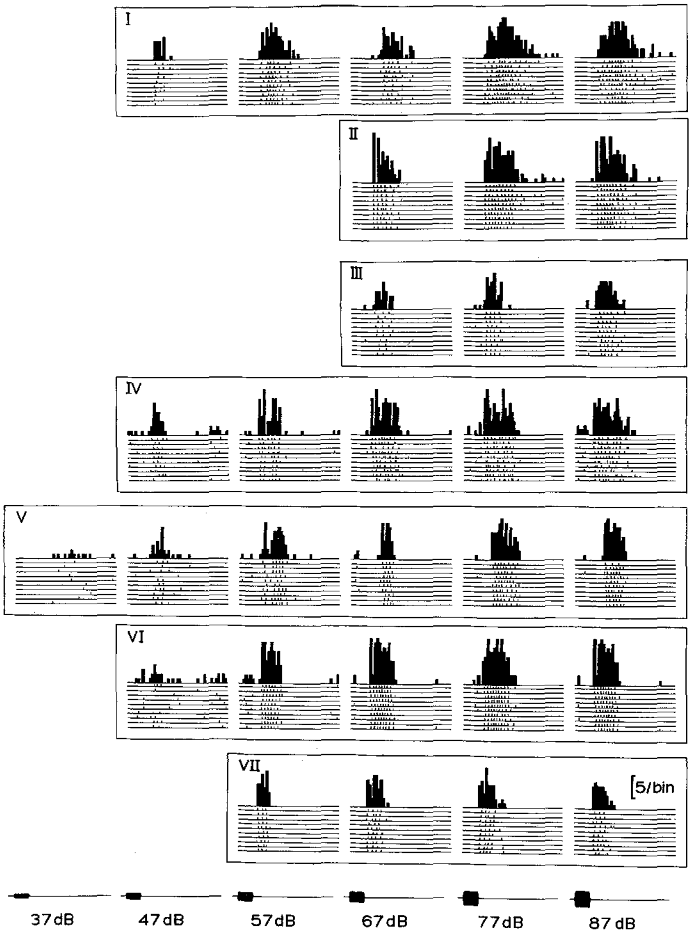

Fig. 1. Comparison of the responses of seven ventral-cord neurons, recorded from the caudal tritocerebrum on one side of a single animal (Experiment LmF 19). For each intensity of the artificial-sound stimulus (white noise, 20 ms duration, repeated at 2/s) 10 individual responses are shown, together with the associated PST histogram (bin width, 3.2 ms). Stimulus marks 20 ms. I, F_2 neuron; II–VI, various C neurons; VII, G_1 neuron

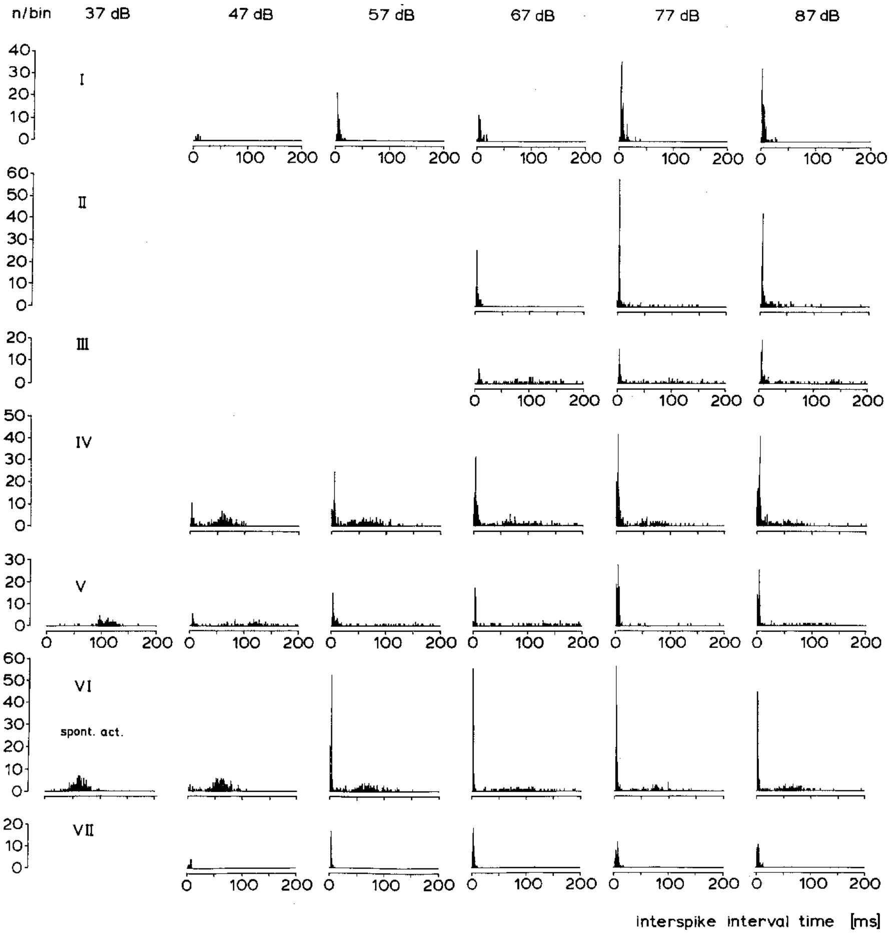

Fig. 2. Interspike-interval histograms of the responses of the neurons of Fig. 1 (Experiment LmF 19). Histograms are composed of 15 samples; bin width, 1 ms. n/bin: number of intervals in each class

vary more widely and the discharge pattern is much less regular.

Taken together, the responses of these 7 neurons reflect only indistinctly the differences in intensity of the stimulus (white noise, 20 ms duration, repeated at 2/s). Certain important neurons are lacking from this sample—for example, the B and K neurons. Nevertheless, considering that 50% of all the neurons at this level of the auditory pathway are represented, one would expect the intensity parameter to be coded more clearly.

But information is contained not only in the direct responses shown in Fig. 1; afterdischarges must also be considered. That these carry information is demonstrated by the interspike-interval histograms obtained for the same neurons over the entire stimulus period of 500 ms (Fig. 2). Here additional differences become apparent, particularly in the neurons with afterdischarge (C neurons, II to VI). The afterdischarge of some of these is pronounced (Neurons IV and VI), while in others it is relatively slight (Neuron II). The neurons without spontaneous discharge (F_2 neuron, I; G_1 neuron, VII) also lack afterdischarge.

The responses of 7 other neurons, most of them of types other than those in Fig. 1, are shown in Fig. 3. Again, these were recorded one after another at a single site (base of the tritocerebrum) in another animal (Experiment LmF 47). This group comprises an F_1 neuron (I), 5 different C neurons (II to VI) and a B_1 neuron (VII). B neurons respond tonically at near-threshold intensities and give phasic on-responses at higher intensities (77 dB, 87 dB). The only type of neuron represented in both experiments is C_2 (Neuron V in Fig. 3 and Neuron VI in Fig. 1). Comparison of the data from all 7 neurons in Fig. 3 shows that this group, as a whole, can clearly distinguish different intensities even without consideration of afterdischarge.

The overall response at high intensities (87 dB) is unambiguously characterized chiefly by the on-responses of the B_1 neuron (VII), the weak, very-long-latency response of the F_1 neuron (I), and the great reduction or elimination of the C_4-neuron response (IV). Sounds at intermediate intensities (67 dB) elicit tonic responses of the B_1 neuron, short-latency responses of the F_1 neuron, and strong responses of the C_4 neuron (IV) that often outlast the stimulus. Low intensities can be characterized by the different response thresholds of the neurons. Even intensity steps between those shown can be discriminated by

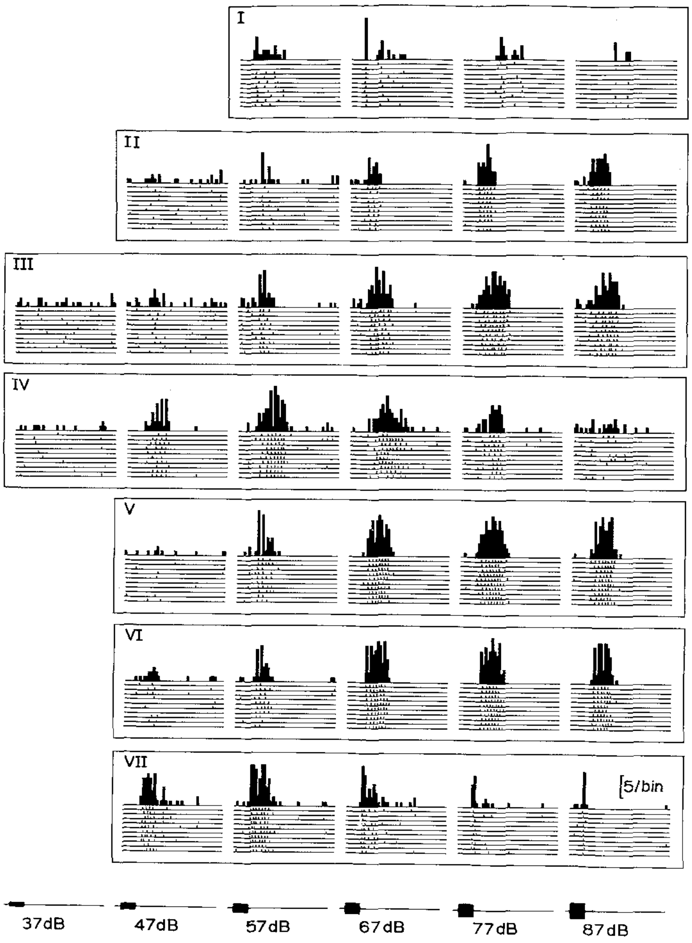

Fig. 3. Comparison of the responses of 7 ventral-cord neurons, recorded from the caudal tritocerebrum on one side of a single animal (Experiment LmF 47). For each intensity of the artificial-sound stimulus (white noise, 20 ms duration, repeated at 2/s) 10 individual responses are shown, together with the associated PST histogram (bin width, 3.2 ms). I, F_1 neuron; II–VI, various C neurons; VII, B_1 neuron

the combined responses of these neurons. These distinctions are also reflected in the differences in latency of the various neurons at different intensities and in the regularity of discharge. Further differences, again, become apparent in the interspike-interval histograms of the complete responses (direct plus afterdischarge; Fig. 4). The F_1 neuron (I), like all F neurons, has neither spontaneous nor afterdischarge. The C neurons II, III and IV have relatively strong afterdischarges, and the discharge in the direct responses is irregular (properties evident in the low amplitudes of the histograms at small intervals); the intervals are broadly distributed. The C_2 neuron (V) and the C_1 neuron (VI), on the other hand, are distinguished by the regularity of the discharge in the direct response; the intervals fall into very few short-time bins, forming leptokurtic histograms. These neurons have relatively little afterdischarge, with a greater scatter of interval times than in the C neurons previously described. The B_1 neuron too has only slight afterdischarge.

The interspike-interval histograms (Fig. 4) illustrate both differences and similarities in the responses of the neurons; resemblances in response suggest similar synaptic connectivities. As examples consider the C neurons II and III, as well as the C_2 neuron (V) and the C_1 neuron (VI); The latter two differ essentially only in their responses to sounds from different directions.

Figure 5 shows the time courses of response of 5 different neurons recorded in another experiment (LmF 26), again at the base of the tritocerebrum. These are, in sequence, a K_2 neuron (I), 3 C neurons (II, III and IV) and a G_1 neuron (V). K neurons give tonic responses to stimuli of up to about 20 ms duration and on-bursts to longer stimuli, so that the direct responses to stimuli of different duration (20 ms and longer) are quite similar. The C_2 neuron (III) in this experiment is of the same type as neurons V in Fig. 3 and VI in Fig. 1 (Experiments LmF 19 and LmF 47, respectively). Type C_4 is represented here by Neuron II and in the data from Experiment LmF 47 by neuron IV (Fig. 3). Type G_1 (neuron V in Fig. 5) was also recorded in another experiment (LmF 19; neuron VII in Fig. 1).

The chief feature of the interspike-interval histograms of this group (Fig. 6) is the clear difference between the complete responses of the K neuron (I) and the C neurons. The K neurons have low-frequency, irregular spontaneous and afterdischarges.

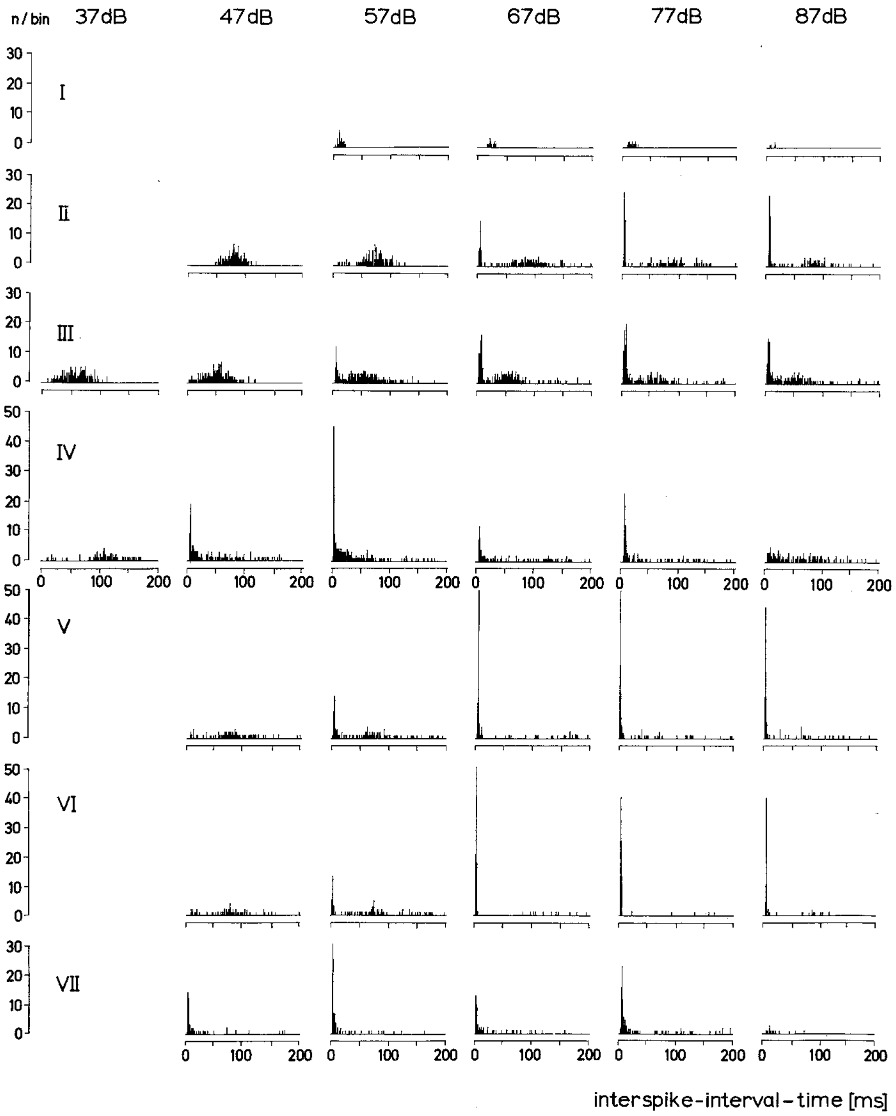

Fig. 4. Interspike-interval histograms of the responses of the neurons of Fig. 3 (Experiment LmF 47). Histograms are composed of 15 samples; bin width, 1 ms. n/bin: number of intervals in each class

The histograms also reveal a distinct difference between the weakly responding C_7 neuron (IV) and the G_1 neuron (V). The direct responses of the two (Fig. 5) are very similar, but the C neuron discharges spontaneously and gives afterdischarges whereas the G neuron does not.

In each of the three experiments presented above the responses of a neuron of Type C_2 were recorded (VI in Experiment LmF 19, V in LmF 47, and III in LmF 26). By comparing the different aspects of the response – direct response and afterdischarge, response magnitude and discharge pattern, latency and threshold – the interindividual variations in response of these three neurons can be determined. The responses are compared graphically in Fig. 7. Small fluctuations appear only in the magnitude of the response (impulses per stimulus); in other respects the responses are quite similar. By extrapolation, we conclude that the other neurons in the three experiments are also fundamentally comparable, so that by combining the responses obtained in one experiment with those from others, the number of neurons to be considered can be appreciably increased. In this way the responses of all the important neurons on one side of the ventral cord can be compared with one another to determine the way in which artificial sounds (white noise, 20 ms duration, repeated at 2/s) at different intensities are coded by the overall auditory system at this level. With this approach, we shall examine the discrimination of 10-dB steps in intensity.

In Fig. 8 the latency-vs.-sound-intensity relationships of neurons from Experiments LmF 47 and LmF 26 are presented. The different latencies at various intensities in themselves could provide discrimination. The most striking differences are those between neuron VII and neuron I at 87 dB in Experiment LmF 47 (40 ms difference in mean latency). This comparison also shows that latency alone is not a suffi-

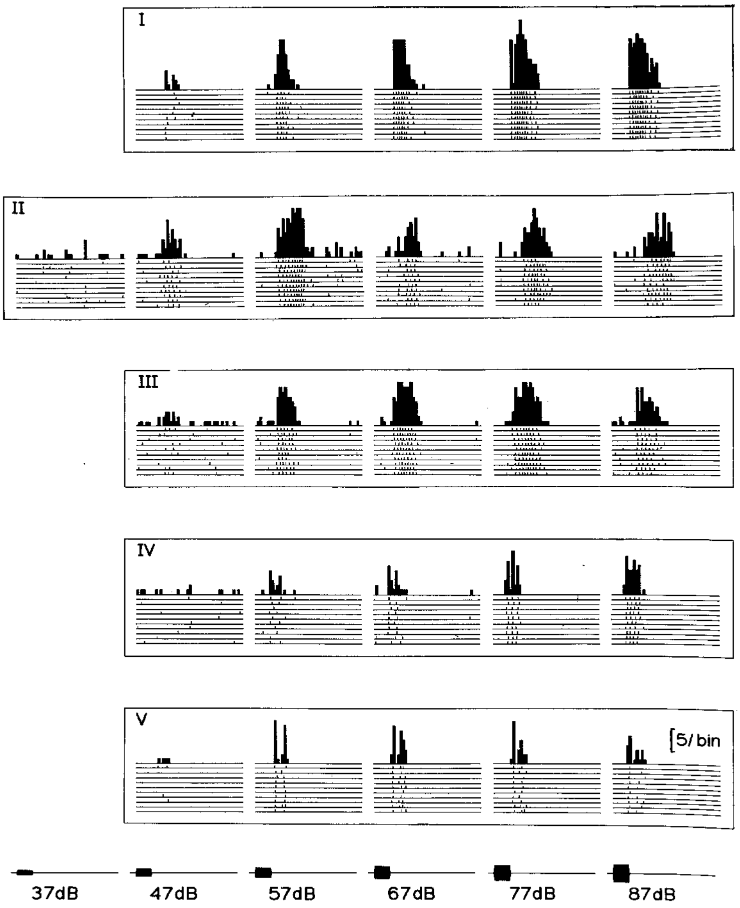

Fig. 5. Comparison of the responses of 5 ventral-cord neurons, recorded from the caudal tritocerebrum on one side of a single animal (Experiment LmF 26). For each intensity of the artificial-sound stimulus (white noise, 20 ms duration, repeated at 2/s) 10 individual responses are shown, together with the associated PST histogram (bin width, 3.2 ms). Stimulus marks 20 ms. I, K_2 neuron; II–IV, various C neurons; V, G_1 neuron

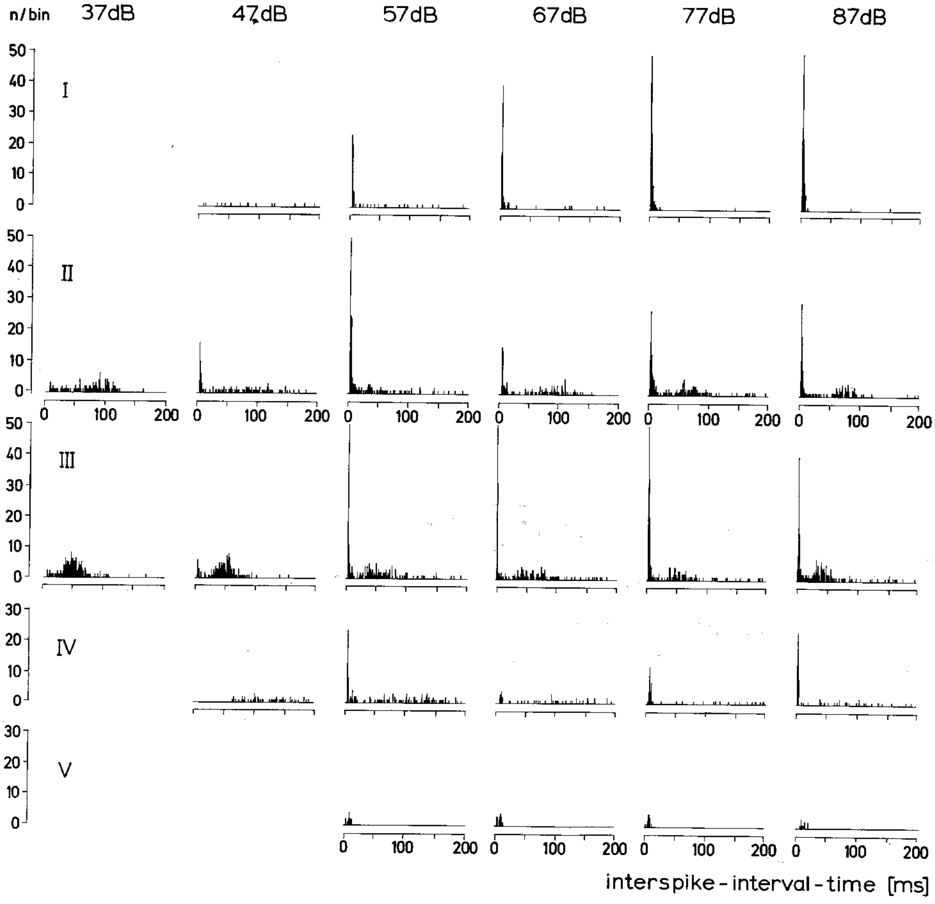

Fig. 6. Interspike-interval histograms of the responses of neurons of Fig. 5 (Experiment LmF 26). Histograms are composed of 15 samples; bin width, 1 ms. n/bin: number of intervals in each class

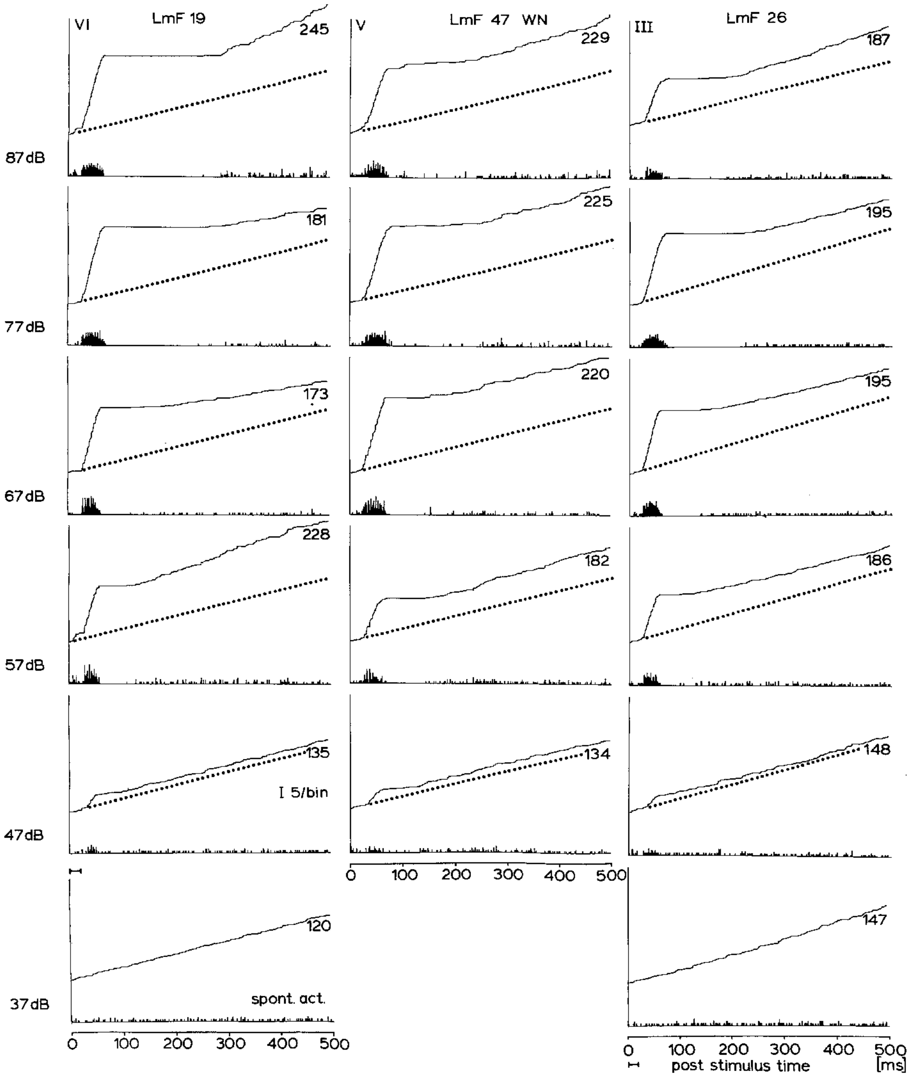

Fig. 7. Comparison of responses of the three C_2 neurons from Experiments LmF 19 (Neuron VI), LmF 47 (Neuron V) and LmF 26 (Neuron III). The PST histograms represent 15 individual responses monitored over the entire stimulus period of 500 ms. Bin width, 1 ms. Above each histogram the curve of the cumulative frequency distribution. Number at the right of each curve represents total impulses in the 15 responses. Curves of the cumulative frequency distribution for spontaneous activity are shown as dotted lines for comparison. Artificial-sound stimuli (white noise, 20 ms, 2/s) at different intensities

cient criterion for assigning a neuron to a certain level in the auditory pathway.

2. *Responses to Simulated Conspecific Songs*

When the conspecific song or a simulation of it is used as a stimulus, the neurons often respond differently than one would expect from their responses to 20-ms bursts of unmodulated white noise. In many cases this occurs even though white noise is used to simulate the song. This difference in effectiveness is associated with the pronounced temporal patterning of the stridulatory song. In *Locusta migratoria* the pattern consists of verses lasting about 330 ms. Each verse is composed of double syllables 30 ms in duration and usually 5 in number, repeated at a rate of about 12/s. It is the temporal structure of the song – including the verse rate – that chiefly affects the magnitude of the neuronal response. An additional parameter that strongly influences the response is the amplitude modulation of the syllables.

Figures 9 and 10 show the responses of the neurons of Experiment LmF 26 to simulations of the conspecific song. The K_2 neuron's responses are largely as would be expected from its responses to artificial sounds. The first part of each double syllable elicits a tonic response, whereas that to the second part is much reduced or absent, because the total duration of the double syllable is greater than 15–20 ms. There is also a reduction in the magnitude of the response to successive double syllables throughout the verse.

With a verse rate of 1/s (Fig. 9, Ib), which corresponds to that of the conspecific song, the responses are distinctly stronger than with a repetition rate of ca. 2/s (Fig. 9, Ia).

The C_4 neuron (Fig. 9, II) responds tonically to artificial sounds (white noise, 20 ms, 2/s; cf. Fig. 5, II). The preferred intensity range is around 57 dB; at higher intensities the responses are weaker but still tonic (see Fig. 5, II and Fig. 6, I). By contrast, simulated songs elicit no response in the intensity range

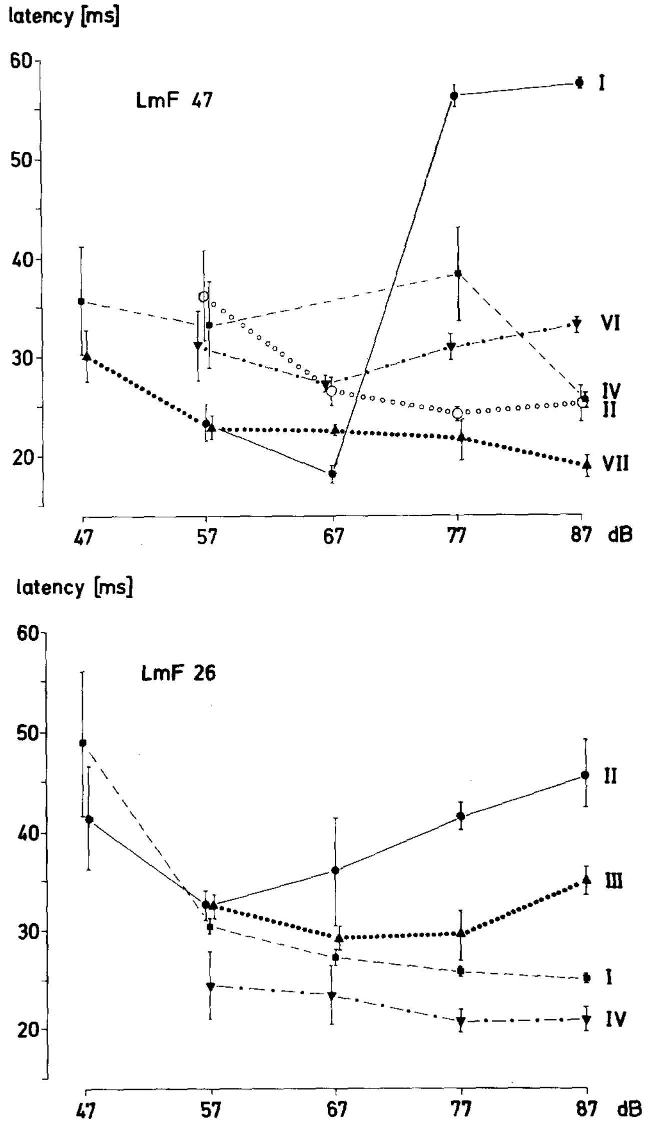

Fig. 8. Intensity dependence of stimulus-response times (latencies) of various neurons from Experiments LmF 47 and LmF 26. Neurons are numbered as in Fig. 3 (LmF 47) and 5 (LmF 26). All values are averages of 18 trials; standard deviations shown as vertical bars. Artificial-sound stimuli (white noise, 20 ms, 2/s) at different intensities

77–87 dB, and the responses at lower intensities are relatively weak (Fig. 9, II)—even at the intensity (57 dB) eliciting the strongest responses to unmodulated white-noise bursts. The C_2 neurons (Fig. 10, III) respond to the individual double syllables as expected; they give tonic responses without discernible habituation. The response is about one-and-a-half to two times as large as that of the K neurons. The C_7 neuron with weak tonic responses (Fig. 9, IV) and the G_1 neuron, which give similar direct responses to artificial sounds (see Fig. 5, IV and V, and Fig. 6), also respond similarly to the simulations of the stridulatory song.

Further information about the responses of the neurons is provided by the interspike-interval histograms (Fig. 11). The K_2 neuron clearly gives stronger direct responses when stimulated with a verse rate of 1/s (Fig. 11, Ib) than with 2/s (Fig. 11, Ia). This is evident in the concentration of intervals in the short-time bins (Fig. 11; cf. the amplitudes of the histograms in Ib and Ia). The "temporal structure" of the verse is also reflected in the interval distribution. Concentrations of intervals at 60 ms and 80 ms correspond to the intervals between syllables. With a tonic response to the double syllable, interval times of 60 ms appear, as in the C_2 neuron (Fig. 11, IIIa and IIIb). The K_2 neuron responds tonically only to the first part of the double syllable (ca. 15 ms), so that here the intervals are concentrated at 80 ms.

The verse interval in a song, for a verse rate of 2/s, is reflected in the concentration of intervals at 260–300 ms (Fig. 11, IIIa and Ia). This implies that during this verse interval there is no discharge. With a verse rate of ca. 1/s (Fig. 11, Ib, II, IIIb, IV and V) the corresponding intervals are about 670 ms; the graphs do not include such large intervals, because normally afterdischarges with intervals of 100–350 ms intervene. The G and F neurons, with no spontaneous activity, are exceptional in this regard. Afterdischarge by the K_2 and C_2 neurons is relatively slight (Fig. 11, Ib and IIb), whereas there is marked afterdischarge of the C_7 neuron and especially of the C_4 neuron (Fig. 11, IV and II). The C_7 neuron and the G_1 neuron (which has no spontaneous activity) differ greatly in their complete responses, as they did in their responses to artificial sounds (Fig. 11, IV and V; see also Fig. 5 and Fig. 6, IV and V).

The suppression of the direct response of the C_4 neuron to simulated songs at high intensities is only one of its response properties (Fig. 9, II, 77 dB and 87 dB). The interval-histogram representation of the complete response (Fig. 11, II) shows that the intervals between verses are filled by afterdischarge at an impulse frequency of about 100/s. A trace of this feature of the response is visible in the histograms for artificial stimuli (Fig. 6, II).

Differences in verse rate affect the direct responses of the neurons. This is illustrated in Figure 12, using the F_2 neuron of Experiment LmF 19 as an example (cf. Fig. 1 and Fig. 2, I, Fig. 9, Ia and Ib). When the verse rate is that of the conspecific song (ca. 1/s, Fig. 12, Ib) the response is considerably stronger than that to simulations at a rate of 2/s (Fig. 12, Ia). However, there is little or no increase in the response when the verse rate is still further reduced (0.5/s; Fig. 12, Ic).

When the song is simulated by modulation of white noise, the C_4 neurons do not respond at 77 or 87 dB, and give only weak direct responses at lower intensities (Fig. 9, III and Fig. 13, III). Simulated

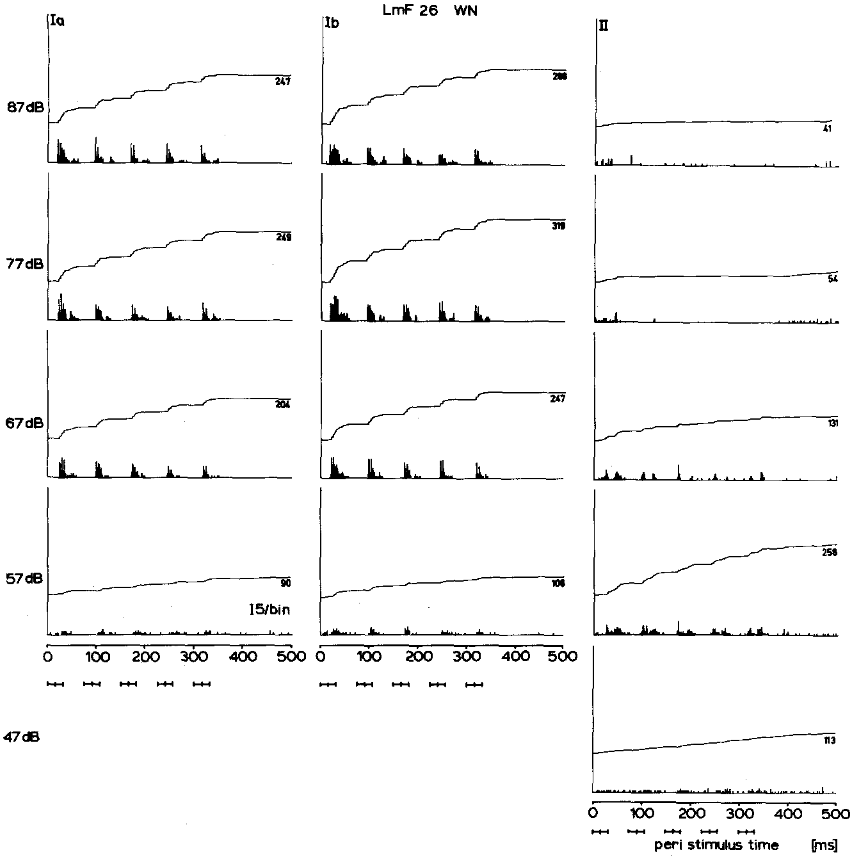

Fig. 9. Responses of the K_2 neuron (I) and the C_4 neuron (II) of Experiment LmF 26 to stimulation with simulated conspecific songs at different intensities (white noise, verse rate 2/s (Ia) or 1/s (Ib and II)). Duration and repetition rate of the double syllables are diagrammed below abscissae (as in all subsequent illustrations of this sort). Graphs include PST histograms of 15 responses monitored for 500 ms after stimulus onset (bin width, 1 ms), and above each of these the curve of the cumulative frequency distribution. At the right of each cumulative curve is the total number of impulses in the 15 responses

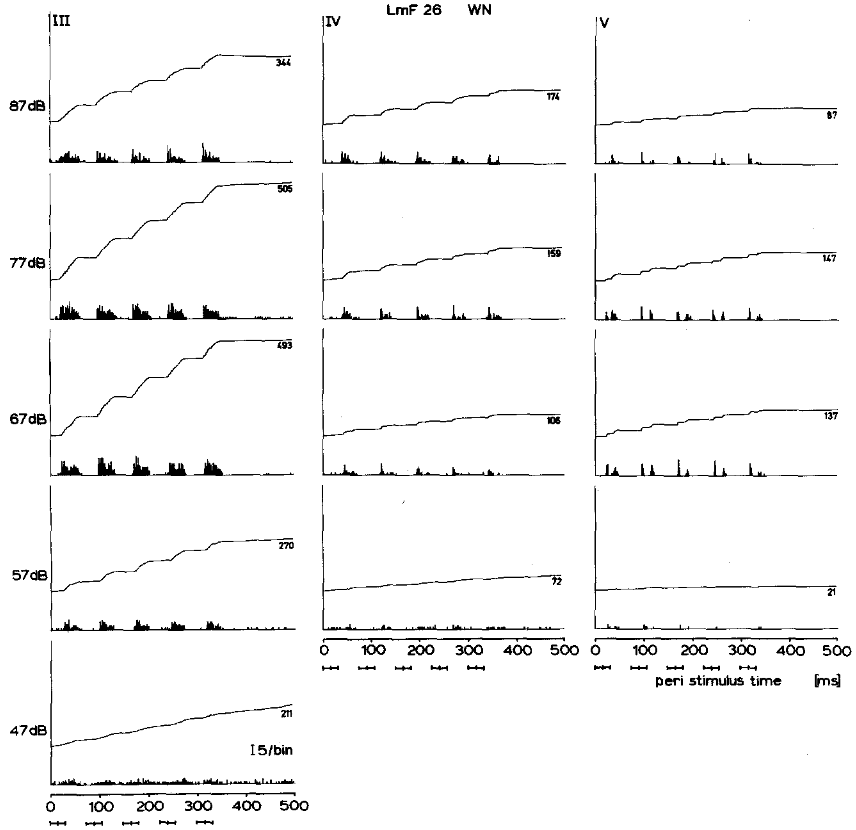

Fig. 10. Responses of the C_2 neuron (III), the C_7 neuron (IV) and the G_1 neuron (V) of Experiment LmF 26 to simulated conspecific songs at different intensities (white noise, verse rate 1/s). Duration and repetition rate of the double syllables diagrammed below the abscissae. Graphs include PST histograms of 15 responses monitored for 500 ms after stimulus onset (bin width, 1 ms), curves of the cumulative frequency distribution and total number of impulses

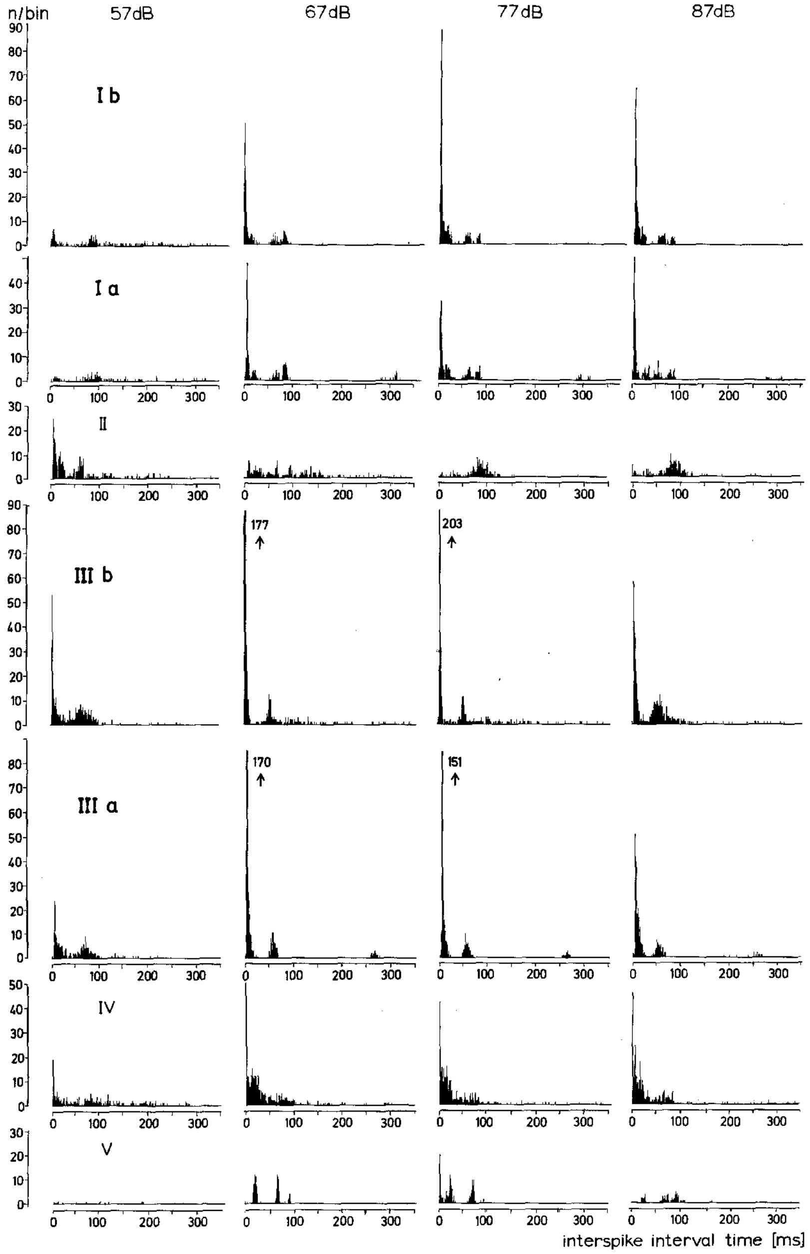

Fig. 11. Interspike-interval histograms of the responses shown in Figs. 9 and 10 (Neurons I–V of Experiment LmF 26). Stimuli were simulated conspecific songs at different intensities (white noise). I, K_2 neuron (Ia, verse rate 2/s; Ib, verse rate 1/s); II, C_4 neuron, verse rate 1/s; III, C_2 neuron (IIIa, verse rate 2/s; IIIb, verse rate 1/s); IV, C_7 neuron, verse rate 1/s; V, G_1 neuron, verse rate 1/s. Each histogram comprises 15 responses (the same as in Figs. 9 and 10); bin width, 1 ms; n/bin: number of intervals in a class

songs with carrier frequencies below 16 kHz elicit similar responses (Experiment LmF 51, Fig. 13, III_{12}). But with carrier frequencies above 16 kHz the direct responses reappear (Fig. 13, III_{30}). Thus the C_4 neurons are identifiable as high-frequency neurons. Neurons with similar responses have been found in the ventral cord of *Decticus verrucivorus* (Rheinlaender and Kalmring, 1973) and *Gryllus bimaculatus* (Wohlers and Huber, 1978).

When neurons of one of the types just discussed were compared with regard to their responses to artificial sounds, there proved to be little or no interindividual variation (Fig. 7, C_2 neurons from Experiments LmF 19, LmF 47 and LmF 26). Both the direct responses and the afterdischarges were similar in pattern, magnitude, threshold, latency and instantaneous frequency. Because of this one would expect the other neurons tested in these experiments to have *comparably* similar responses. They can all be considered together, making up all "full complement" of auditory neurons for the ventral-cord region on one side of the animal. The coding of sound signals in the "overall auditory pathway" at the ventral-cord level can thus be determined.

In Fig. 14 the responses of the 8 most important neurons on one side of the ventral cord are summa-

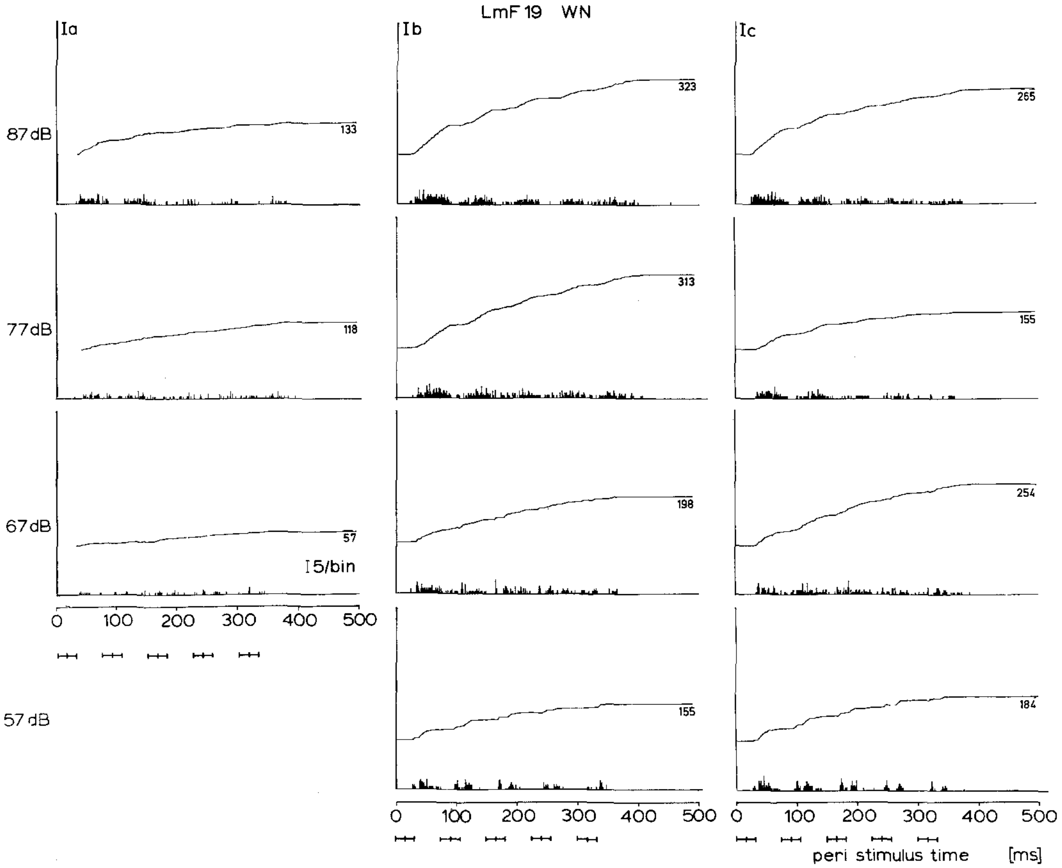

Fig. 12. Comparison of responses of the F_2 neuron (I) of Experiment LmF 19 to stimuli differing in verse rate. Ia, 2/s; Ib, 1/s; Ic, 0.5/s. Stimuli were simulated conspecific songs (white noise) at different intensities. PST histograms comprise 15 responses monitored for 500 ms after stimulus onset (bin width, 1 ms); above them curves of cumulative frequency distribution and total number of impulses

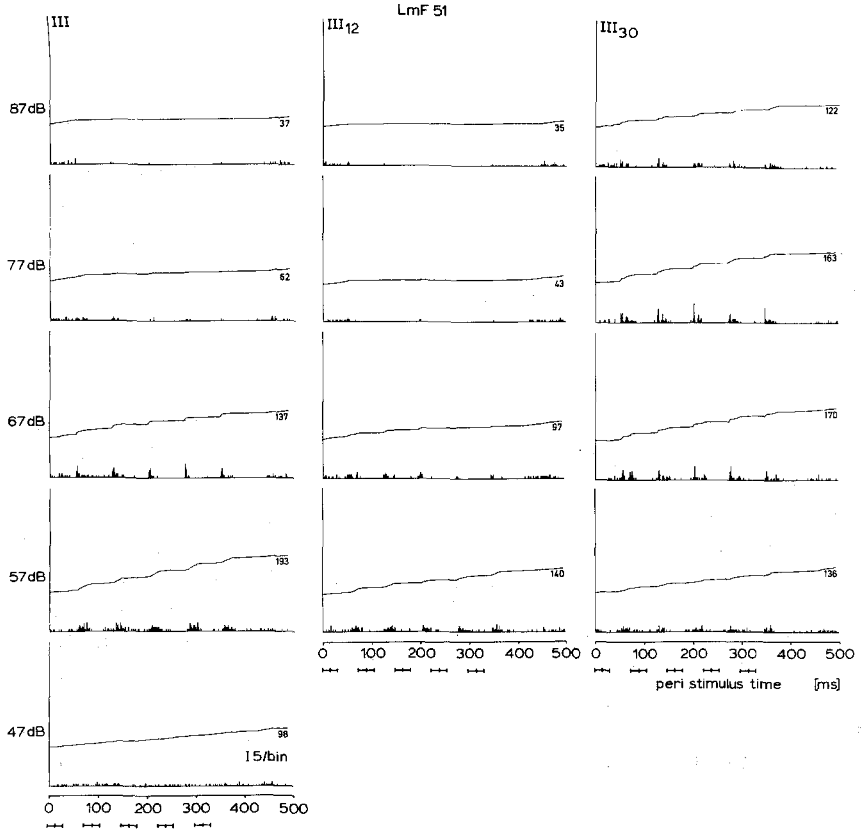

Fig. 13. Comparison of responses of a C_4 neuron of Experiment LmF 51 to simulated conspecific songs with different carrier waveforms: white noise (III), 12 kHz (III_{12}), and 30 kHz (III_{30}). PST histograms comprise 15 responses monitored for 500 ms after stimulus onset (bin width, 1 ms); above them curves of the cumulative frequency distribution and total number of impulses

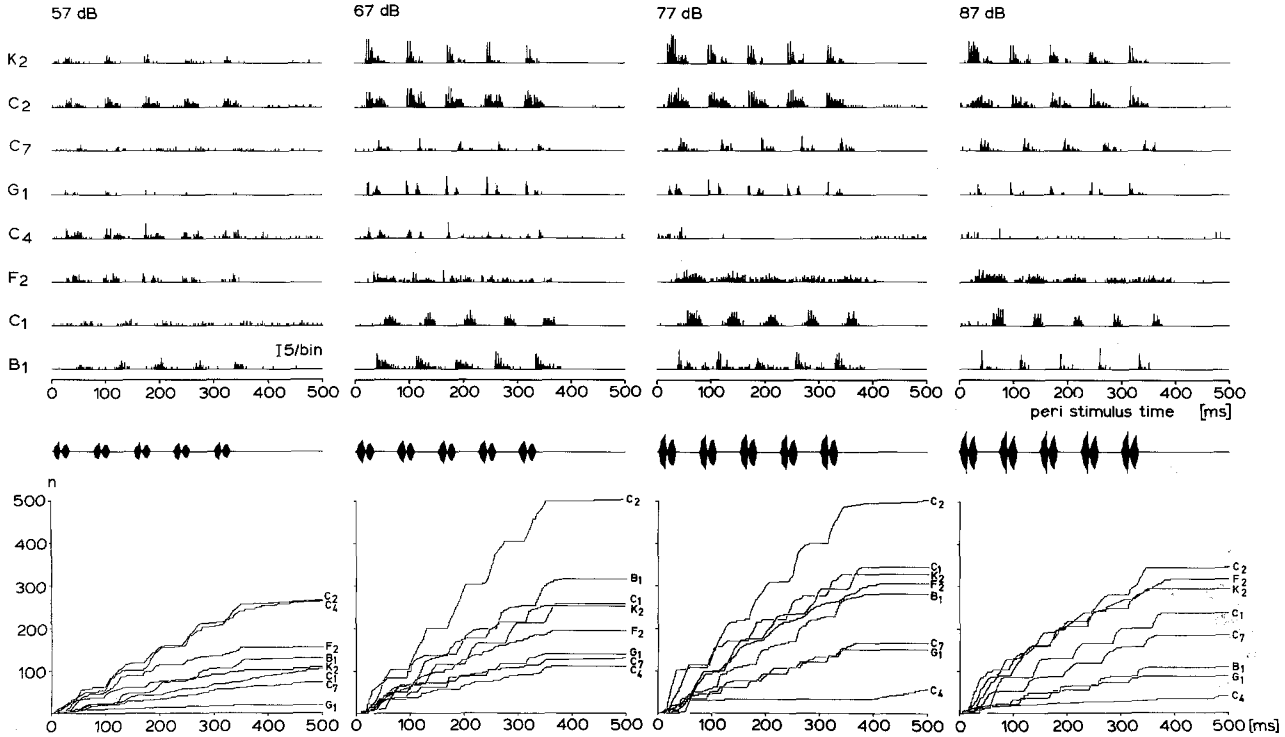

Fig. 14. Comparison of the responses of 8 ventral-cord neurons to identical stimuli, simulated conspecific songs at different intensities (white noise, verse rate 1/s). Responses shown as PST histograms of 15 responses, monitored for 500 ms after stimulus onset (bin width, 1 ms). K_2, C_2, C_7, G_1 and C_4 neurons from Experiment LmF 26; F_2 neuron from Experiment LmF 19; C_1 neuron from Experiment LmF 51; B_1 neuron from experiment LmF 47. Lower part: curves of cumulative frequency distribution for each intensity. n: total number of impulses in the 15 individual responses

rized in terms of PST histograms and cumulative discharge curves. The stimuli were simulated conspecific songs (white noise, verse rate 1/s) at 4 different levels of intensity. The figure is limited to 8 of the approximately 15 neurons on each side for clarity of presentation. These neurons were selected for their particularly characteristic responses. The various responses of the remainder resemble those of one or more of the neurons illustrated, and if included would not appreciably change the general picture; they enhance or supplement the coding performance shown here.

The combination of the direct responses of these 8 neurons guarantees discrimination of the 4 intensity steps. Moreover, the "temporal structure" of the songs—syllable substructure and duration, intervals between the individual syllables, verse duration—can be resolved by the totality of neuronal activity. The components of the double syllable are reflected in the responses of the G_1 neuron and to some extent in those of the C_7 neuron. The first part of the double syllable is "represented" in the responses of the K_2 neuron; the duration of the whole double syllable is integrated in the tonic response of the C_2 and C_1 neurons. The responses of the F_2 neurons considerably outlast the double syllables. Similarly, the differences in latency among these neurons can be crucial factors in coding; this point is brought out by the cumulative curves.

Discussion

In the experiments described here we have examined the coding properties of the auditory pathway at the level of the ventral-cord neurons ascending to the supraesophageal ganglion. As far as is known, there are 15 of these neurons on each side of the ventral cord in *Locusta migratoria*. According to all previous studies these neurons have two basic functions (Kalmring, 1975; Kalmring et al., 1978; Čokl et al., 1977).

In their postsynaptic regions they receive and process information from the receptor organs on the two sides. The responses of the ventral-cord neurons, as a rule, are more complex than those of the receptor cells. Certain parameters of sound signals, such as direction and temporal structure, are more distinctly coded than others. There are neurons that respond only to ipsilateral sound within an angular range of 120° (the F neurons). At this level of the auditory pathway, for the first time, various neurons exhibit habituation. Coding of frequency and intensity is also improved in the ventral-cord-cell responses, as compared with the receptor level.

The second important function is the distribution of this processed information to many higher processing centers in ventral cord and supraesophageal ganglion. The responses are conducted unchanged along the main trunk of the axon to the supraesophageal ganglion; spatially and temporally variable filter processes can take place only at axonal branch points.

The situation is the same in the ventral cords of crickets (Huber, 1977; Hill and Boyan, 1977; Elsner and Popov, 1978) and tettigoniids (Rheinlaender and Kalmring, 1973; Rheinlaender, 1975).

Most of the higher processing centers are multisensory neuropile regions which receive input from other sensory systems as well. The projection areas of the ventral-cord neurons are to a considerable extent superimposed there (Rehbein, 1976; Bauer, 1977). Thus convergence is very likely to be a property of the further information processing in these neuronal centers.

The preprocessing of information in the postsynaptic regions of the ventral-cord neurons causes no loss of total information as compared with the receptor level. Certain sound parameters – particularly the temporal structure of the conspecific song – are emphasized in the responses of various neurons, but there is not at this level a "neuronal filter" that detects and passes only species-specific communication sounds. Coding is far more comprehensive than would be required for detection and recognition of the conspecific song. The information the receptors provide about sound signals from the environment is preserved as a basis for subsequent processing. Such processing of the signals from the ventral-cord neurons enables recognition and localization of a stridulating animal of the same species, which behavioral experiments have shown to be within the animal's capabilities (Huber, 1975). Moreover, other noises in the animal's surroundings can be detected and analyzed – a function in some cases crucial to survival. The mechanisms and potentialities of these higher-order processes are as yet unknown.

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