Auditory nerve and interneurone responses to natural sounds in several species of cicadas

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ABSTRACT. The calling and courtship songs of 17-year cicadas and of Say's cicadas differ both in the sound frequency spectrum and in temporal pattern. Multiunit recordings with hook electrodes from the whole auditory nerve show that the hearing organs are especially sensitive to transient stimuli occurring in natural sounds. Artificially produced clicks elicit bursts of spikes synchronized among various primary sensory fibres. These fibres respond to natural calling and courtship songs with a specificity dependent on carrier frequency, rhythm and transient content of the sound, following sound pulses (i.e. tymbal actions) up to repetition rates of 200 Hz. An ascending, plurisegmental interneurone was characterized by intracellular recording and simultaneously stained with cobalt. Its main arborization spatially overlaps the anterior part of the sensory auditory neuropile, and the axon was traced as far as the prothoracic ganglion. Direct input from primary auditory fibres was suggested by latency measurements. Intracellular recordings from such neurons in different species show distinct auditory input, with phasic-tonic spike responses to tones. In general, the interneurone response is more species-specific to calling than to courtship songs, and the preferential response to the conspecific calling song is based primarily upon sound frequency content.

Introduction

Cicadas have been used to study sound communication in insects (see Alexander, 1960). In most species only the males produce sounds (Pringle, 1954, 1957; Popov, 1975), while both sexes possess hearing organs (Vogel, 1923; Michel, 1975; Young & Hill, 1977).

Sound reception at the level of the auditory nerve has been previously investigated in several species of cicadas, showing the response to the temporal structure of the song (Pringle, 1954), to pure tones and to clicks (Enger *et*

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al., 1969). Threshold curves show an optimal auditory sensitivity correlated to the sound spectrum of the conspecific song (Katsuki, 1960; Katsuki & Suga, 1960; Enger *et al.*, 1969; Simmons *et al.*, 1971; Young & Hill, 1977).

The course of the auditory nerve and its central projections have been studied by Wohlers *et al.* (1979); this anatomical work provided a background for the physiological investigations reported in this paper, where responses to natural calling and courtship songs were recorded either extracellularly from the whole auditory nerve or intracellularly from an identified ascending interneurone.

Materials and Methods

Adult 17-year cicadas, *Magicicada septendecim* (L.), *M.cassini* (Fisher), *M.septendecula* (Alexander & Moore), were collected in June 1978 in Botecourt Co., Virginia, and Say's cicadas, *Okanagana rimosa* (Say), with a life cycle of 8–10 years, in July in Montmorency Co., Michigan. All specimens were caged on potted cistena plum shrubs (*Prunus* sp.) where they could feed, and where females could oviposit. The cicadas were transported to the laboratory in Ann Arbor.

For electrophysiological studies the animals, with the legs and wings removed, were mounted upside down on a rigid platform. The nervous system was then exposed from the prothoracic ganglion caudal to the area of the sternal canal (Vasvary, 1966). A silver platform serving as an indifferent electrode was positioned under the fused metathoracic-abdominal ganglionic complex for support. Fielden's ringer (Fielden, 1960) replaced the haemolymph.

Auditory nerve recordings (Fig. 1, lower left) were carried out with hook electrodes (40-μm steel wires), placed approximately 8 mm from the hearing organ. The nerve was gently lifted out of the saline solution and cut near the ganglion to eliminate efferent activity caused by motoneurones (Wohlers *et al.*, 1979). Vaseline was then placed on the exposed nerve to prevent dehydration.

Auditory interneurones were located in the metathoracic ganglion and penetrated intracellularly (Fig. 1, CE). 3-M potassium-acetate-filled microelectrodes (30–50 megohms) were used for prolonged studies of responses (more than 30 min), while 30% cobalt-nitrate-filled electrodes served simultaneously to record and
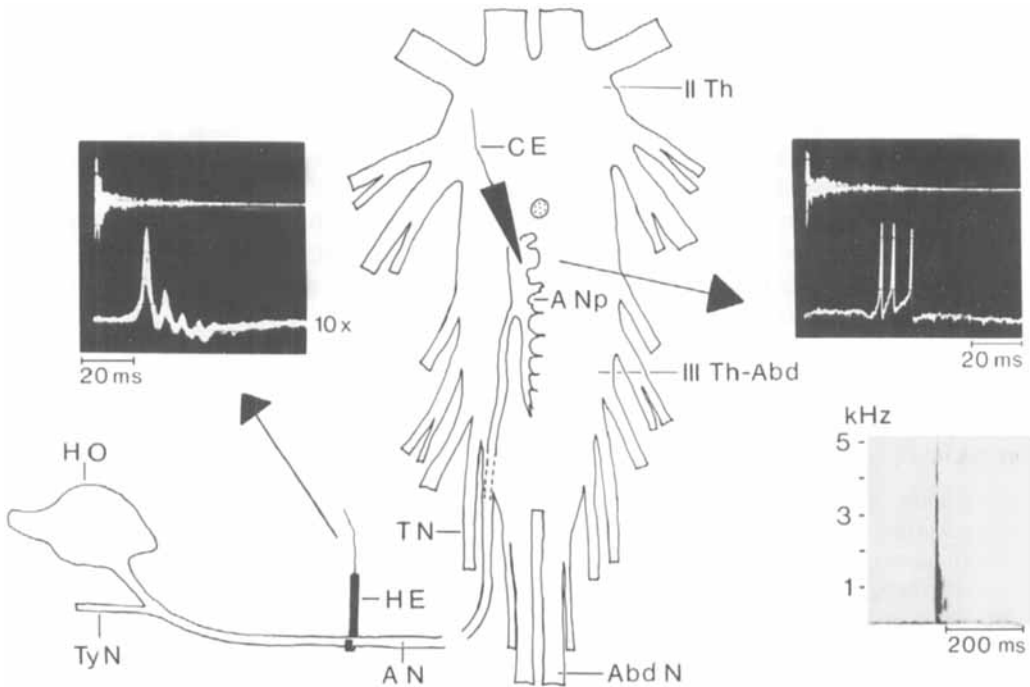

FIG. 1. Schematic drawing of the mesothoracic (II Th), metathoracic (III Th) and abdominal (−Abd) ganglionic complex of a male 17-year cicada (middle) showing the two recording sites: extracellular hook electrode (HE) recording from the cut auditory nerve (AN), and intracellular recording (CE) from an interneurone in the anterior region of the auditory neuropile (ANp) within the metathoracic ganglion. Abd N, abdominal nerve; HO, hearing organ, TyN, nerve branch to tymbal muscle; TN, tensor nerve. *Insets.* Upper left – auditory nerve responses (ten superimposed sweeps, lower trace) to 'click' sounds produced by human mouth (upper trace). Upper right – interneurone response (lower trace) recorded intracellularly to a single 'click' sound (upper trace). Lower right – sound spectrogram of such a 'click'.

stain the neurones. Details of the methods were similar to those described by Wohlers & Huber (1978). Stained cells were intensified using the Timm's technique, modified by Bacon & Altman (1977). Treated ganglia were embedded in soft Araldite, and thick sectioned (40 μm). Reconstructions were made on a Wild M20 microscope equipped with a drawing tube.

Acoustic stimuli were of three types. *Tick sounds* ('*clicks*'), produced by the human mouth, of short duration (< 20 ms; exponential decay) and covering frequencies from a few Hz to more than 6 kHz (Fig. 1, audiospectrogram, lower right). *Pure tones* (500 Hz to 10 kHz), delivered through a Nagra (Kudelski) Model DH amplifier and speaker located 130 cm from the hearing organs. *Natural songs*, presented from a magnetic tape (15 i.p.s) using a Magnecord tape recorder (Model PT 63-A2HZ) and amplifier (Model PT 63-J) with speaker also located 130 cm from the hearing organs.

Data were stored on a Racal Store 4D tape recorder and analysed from Polaroid pictures and oscilloscope films. Audiospectrograms (sonograms) of the various acoustical stimuli were made using a Kay Vibralyzer 7030 A Sound Spectrum Analyser (range 1—16 kHz). A General Radio Company Sound and Vibration Analyzer Type 1564A was used to measure the sound intensities in dB SPL (0 dB = 2×10^{-5} Newton/m^2) at the location of the hearing organ. No attempt was made to differentiate between ipsi- and contralateral sound intensities.

Results

Biological aspects

The three species of 17-year cicadas live sympatrically and are intermingled individually. Within the brood we observed in Botecourt Co., Virginia, individuals of the same and of different species often fed and oviposited only 10—15 cm apart (see Dybas & Davis, 1962), though according to Alexander & Moore (1962) there is no sign of cross-copulation and hybridization. The three species can be distinguished through differences in acoustical behaviour, and their songs are among the most specialized of North American cicadas.

The males produce three types of sound signals (Moore & Alexander, 1956; Alexander & Moore, 1958): a *calling song*, consisting of buzzes and/or ticks emitted either individually or in chorus, is responsible for activating and assembling both males and females; a *courtship song* ('*sound*') also consisting of buzzes and/or ticks and produced by individual males when approaching and contacting other individuals, usually females; a *disturbance sound* ('*squawk*') when startled into flight or restrained in any way.

Based on audiographic studies (Alexander & Moore, 1958) the frequency spectrum and the pulse rate (i.e. rate of tymbal actions), as well as the occurrence of buzzes and ticks varies in characteristic fashion (Table 1). In addition to these differences in temporal pattern and frequency spectra of each song type, there are also differences in the manner of flight and chorusing. After one to several calling phrases, *M.septendecim* undergoes a bout of flight whereas *M.cassini* and *M.septendecula* fly, or at least flip their wings, usually after each phrase (Alexander & Moore, 1962). In the field, synchronized chorusing and flight in *M.cassini* need warmth and sunshine. Chorusing usually begins around 13.00—14.00 hours local time and continues throughout the afternoon (Alexander & Moore, 1962; Heath, 1967).

Okanagana rimosa is a species with the individuals spaced less densely, but usually within a rather limited area. They often broadly overlap geographically and seasonally with 17-year cicadas. In 1978 in Montmorency Co., Michigan, an area of 3×50 m was occupied by about 200 individuals, and the next population was several kilometres away. The calling and courtship songs are uniform; they vary in duration (Table 1), and contain nearly equally spaced pulses (paired tymbal actions). Each audiospectrographic pulse of sound (see Fig. 6, 3) is composed of 2—4 sound bursts from 2—4 tymbal ribs in each tymbal, resulting in a total of 5—8 sound bursts/pulse (per paired action of both tymbals, Fig. 6, 1).

Electrophysiological studies

Extracellular recordings were carried out from the auditory nerve, usually ipsilateral to the sound source. This nerve contains at least

TABLE 1. Sound parameters from various songs of the three 17-year cicadas (*Magicicada*) and of Say's cicada (*Okanagana rimosa*) (after Alexander & Moore, 1962, in part). In all species mentioned in the table each sound pulse is composed of 2–7 bursts of sound produced by the inward buckling of 2–7 sclerous ribs in each tymbal for each muscle contraction.

Species*	Frequency range (kHz)		Temporal structure (rhythm)
	Carrier	Main sound	
Calling songs			
M. sept.	1–2	1–2	Buzzes (duration 2–4 s) separated by pauses of 0.5–2.0 s; buzzes composed of pulses (120–160/s), each pulse represents one contraction of a tymbal muscle and its resulting tymbal and abdominal vibrations.
M. cass.	4–12	4–6	A series of 12–40 ticks (duration 10 ms) delivered at 16–25/s followed by a buzz (duration 1–2 s). Pulse rate within the buzz 180–210/s.
M. sptd.	4–14	4–6 buzzes 6–12 ticks	A series of alternations between buzzes and ticks (25–35 buzzes and ticks) with steadily increasing intensity and rate, followed by ticks (18–24) of rather constant intensity and rate (no buzzes). Pulse rate within buzzes 130–150/s.
O. rim.	6–12	7–11	Continuous-sounding buzz (duration up to 1 min) composed of double pulses (duration 6–8 ms) produced at rate of 70–84/s; each double pulse produced by combined close alternation of both tymbals. Rather constant intensity.
Courtship songs			
M. sept.	1–3	1–2	Short buzzes (duration 40 ms), rate 5/s.
M. cass.	4–14	5–8	A series of double ticks (durations 20–25 and 15–25 ms) separated by 20–25 ms; rate 6–7/s.
M. sptd.	4.5–14	5–9	Ticks (duration 80–120 ms); rate 3–5/s.
O. rim.	4.5–15	6–12	Temporal structure (rhythm) as calling song, but of shorter duration (up to 1 s) and increasing intensity.

* See Methods for full names.

1300 primary auditory sensory fibres (Michel, 1975; Young, 1975). This large number of axons within a nerve 60 μm in diameter greatly complicates unravelling the function of single primary auditory fibres. Intracellular recordings were obtained from interneurones responding to natural sounds, but only those recordings which lasted at least 30 min were evaluated.

Auditory nerve recordings

Tick sounds (clicks) were produced by the human mouth at intensities of 70–80 dB SPL (Fig. 1, inset, upper left). They covered a frequency range from a few Hz up to more than 6 kHz, with the main sound energy being delivered in the range of 500 Hz to 2 kHz (Fig. 1, inset, lower right). Clicks elicited bursts of spikes which summed to compound action potentials (Fig. 1, inset, upper left, lower trace). The response most commonly exhibited 3–4 peaks spaced about 5–6 ms apart. The decrease in peak amplitude with time suggests a reduction in the number of actively participating primary auditory fibres with time, and that the response reflects the decreasing amplitude of the signal. All species tested responded similarly. In 17-year cicadas the latency of the response to clicks varied from 18 to 22 ms, while *O. rimosa* showed latencies of 20–23 ms.

In our set-up, the sound-travel time from the speaker to the hearing organs was 4 ms (distance 130 cm). Given this, a transduction time of 1–2 ms, and the distance of 8 mm from the hearing organ to the recording site in the auditory nerve, the conduction velo-

city was calculated as between 0.5 and 0.6 ms. This low velocity agrees with the small diameter of the primary auditory fibres (< 1 μm).

In the four species tested, the inter-ear distance is *c.* 1 cm, resulting in a sound-travel time of 30 μs between the two hearing organs. No time difference was measurable in the auditory nerve responses to clicks when recording from both auditory nerves simultaneously. The compound action potentials of both nerves usually had very similar shapes, showing the same number of peaks in decreasing amplitude with time.

Click sounds also gave rise to interneuronal responses (Fig. 1, inset, upper right) which most commonly contained 3–4 spikes. The inter-spike intervals are not necessarily equal to the inter-peak intervals of the auditory nerve response.

Pure tones elicited a few compound action potentials (peaks) of decreasing amplitude followed by a more or less sustained low amplitude discharge. Similar 'phasic–tonic' responses were described by Enger *et al.* (1969) in a Brazilian cicada. Although our set-up was not calibrated for measuring threshold curves, we could roughly determine the best sound frequency responses and compare them with the optimal auditory sensitivities measured by Simmons *et al.* (1971), see Table 2. Tone pulses also excited auditory interneurones (Fig. 7, 1).

Natural sounds were preferred for the study

TABLE 2. Best auditory sensitivity in two 17-year cicadas, stimulated at 85 dB SPL

Species	Optimal sound frequency (kHz)	
	Simmons *et al.* (1971)	Present observations
M.septendecim	1.5–2.5	2
M.cassini	2.5–5.0	3–5

of the specificity of auditory nerve and interneuronal responses. Fig. 2 (1, lower trace) shows compound auditory nerve potentials in response to the playback of the conspecific calling song from *M.septendecim*. An initial burst of compound action potentials (arrow) is followed by a rather irregular discharge of many primary auditory fibres. The calling song also excited an auditory interneurone (Fig. 2, 2, lower trace). Here the phasic components indicated by grouping of spikes (arrows) are much more pronounced and may reflect fast amplitude modulations in the song.

Specificity of auditory nerve responses

The comparison of auditory nerve responses to conspecific and allospecific calling songs presented at 80 dB SPL (Fig. 3) revealed some remarkable differences. *M.septendecim* showed the highest degree of activation in response to the conspecific calling song (Fig. 3, 1 left),

M.septendecim   85 dB
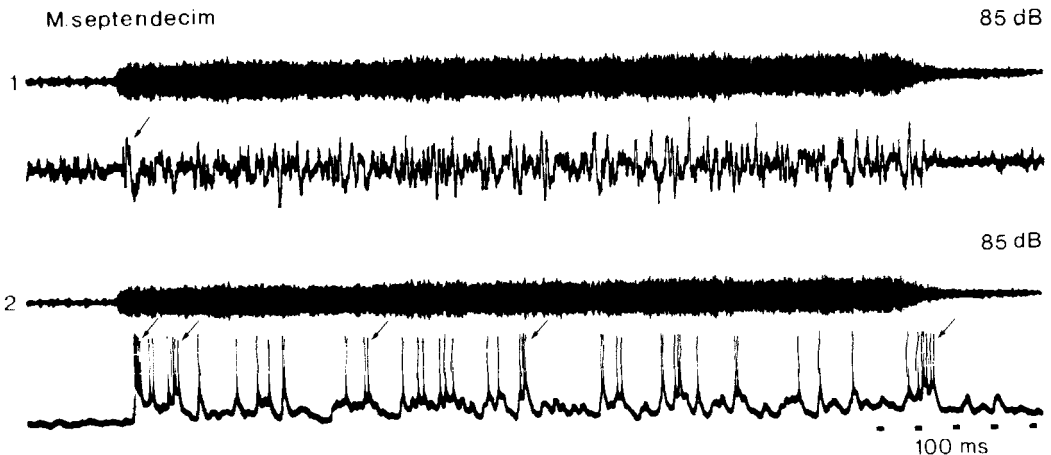

FIG. 2. Oscillograms of auditory nerve (lower trace in 1) and interneurone responses (lower trace in 2) to conspecific calls of *M.septendecim* (upper traces in 1 and 2) presented at intensities of 85 dB SPL. Arrows point to bursts of spikes caused by sudden amplitude modulations in the song.
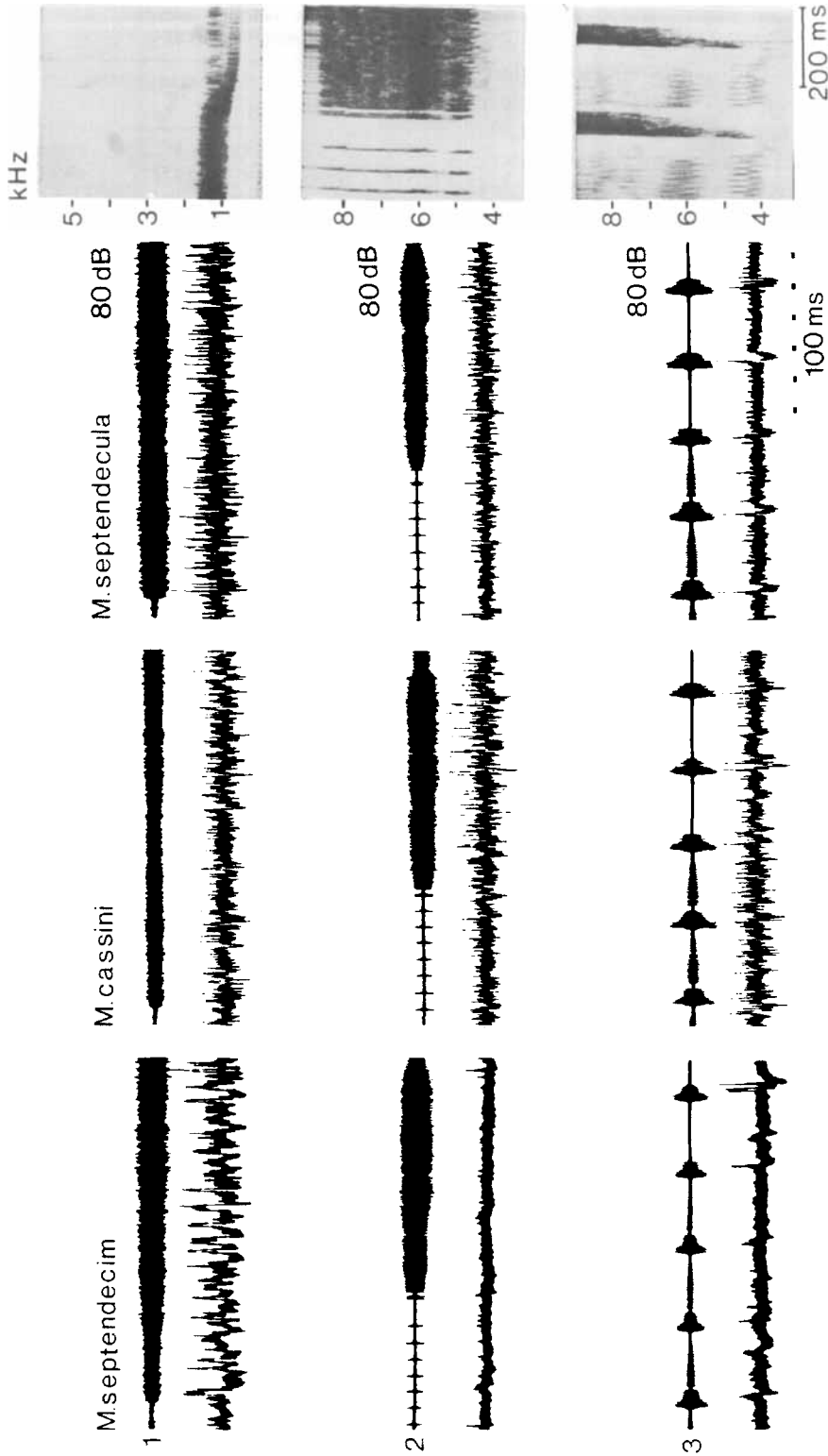
FIG. 3. Auditory nerve responses (lower traces in each oscillogram) recorded from *M. septendecim* (left column), *M. cassini* (middle) and *M. septendecula* (right) to calling songs presented at intensities of 80 db SPL (upper traces in each oscillogram). Calls (upper traces in each row) are from *M. septendecim* (1), *M. cassini* (2), *M. septendecula* (3). Right, corresponding sound spectrograms.
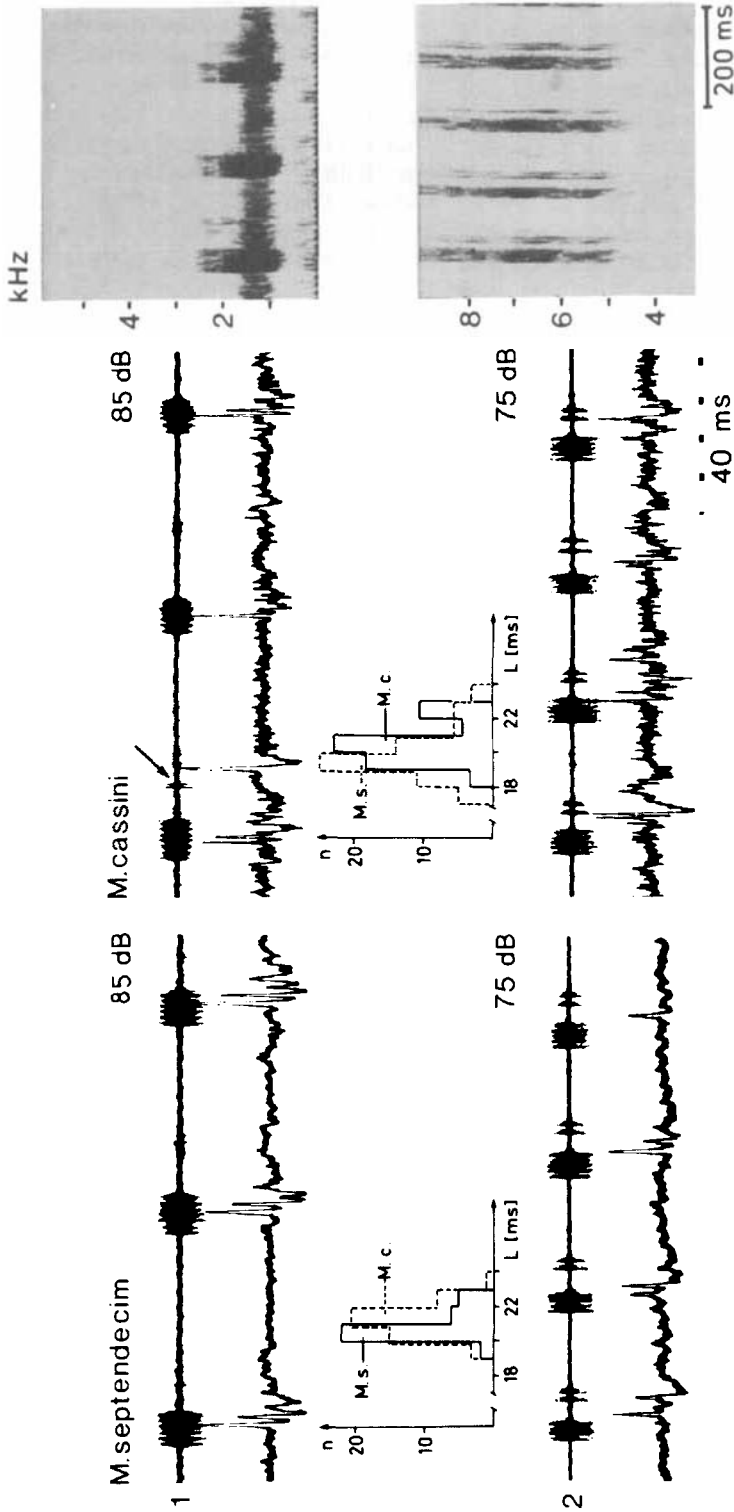
FIG. 4. Auditory nerve responses (lower traces) of *M.septendecim* (left column) and *M.cassini* (right column) to courtship buzzes of *M. septendecim* (upper traces, 1) and to courtship ticks of *M.cassini* (upper traces, 2). Right, corresponding sound spectrograms. Stimulus intensities 85 (1) and 75 (2) db SPL. Insets, latency (L in ms) histograms of the responses of both species to the courtship song of *M.septendecim* (left) and of *M.cassini* (right); n, number of courtship buzzes (left) or ticks (right); *M.s., M.septendecim; M.c., M.cassini*

whereas *M.cassini* and *M.septendecula* calls elicited only weak responses, if any, in the *M.septendecim* nerve (Fig. 3, 2 and 3 left). This 'preference' for the conspecific song must be due to the tuning of the *M.septendecim* hearing organ to the low frequency components of its call (Fig. 3, sound spectrogram, top right; see also Simmons *et al.*, 1971). Furthermore, the hearing organ is also sensitive to transients, as indicated in the weak response to *M.septendecula* ticks (Fig. 3, 3 left), even if their carrier frequency does not overlap that of the conspecific song.

In *M.cassini* and *M.septendecula* there seems to be no 'preference response' to the conspecific call (cf. Fig. 3, middle and right columns). In *M.cassini* and *M.septendecula* calls, the absence of a preference response is understandable, because both species emit calling songs with widely overlapping frequency spectra (Fig. 3, corresponding sound spectrograms). Nevertheless, there are also small differences in the auditory nerve responses between the two species, which indicate that the temporal structure of the conspecific song is more precisely copied (Fig. 3, cf. 2 middle with 3 right).

The *M.cassini* and *M.septendecula* responses to the calls of *M.septendecim* (Fig. 3, 1, middle and right) are not understood. They cannot result from a tuning to the low frequency part of the *M.septendecim* call, because in this range (1–2 kHz) the *M.cassini* hearing organ is 50 dB less sensitive than that of *M.septendecim* (Simmons *et al.*, 1971).

The courtship sounds of the three species of 17-year cicadas are composed of buzzes and/or ticks, differing in duration and rate (see Table 1). Fig. 4 shows parts of courtship songs of *M.septendecim* (1, upper traces) and *M.cassini* (2, upper traces) and corresponding sound spectrograms (right). There is no clear difference in the auditory nerve response of *M.septendecim* (Fig. 4, 1 and 2, left column, lower traces) or *M.cassini* (Fig. 4, 1 and 2, right column, lower traces) to conspecific and allospecific courtship sounds. The 'stronger' response of *M.septendecim* to the conspecific song is partly due to a 10 dB higher intensity of the stimulus. Within the *M.cassini* courtship song (Fig. 4, 2, left column) the second tick within a double tick (Table 1) elicited no response in the *M.septendecim* ear, whereas the *M.cassini* ear (Fig. 4, 2, right column)
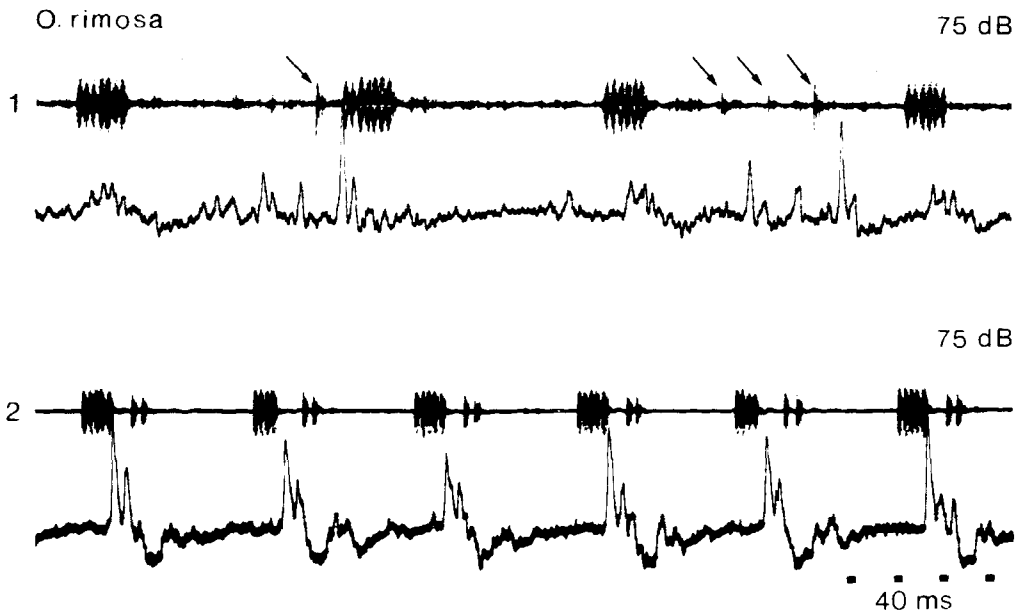
O. rimosa   75 dB

75 dB

40 ms

FIG. 5. Auditory nerve responses of *O.rimosa* (lower traces in 1 and 2) to *M.septendecim* (1) and *M. cassini* (2) courtship songs (upper traces in 1 and 2). Arrows point to sharp transients which originate from wing flipping, and which differ from the buzzes of *M.septendecim* in sound frequency content. Stimulus intensities 75 dB SPL.

frequently copies the second tick too. The arrow in Fig. 4 (1, right column) points to a sharp transient which was on the stimulus tape but did not belong to the *M.septendecim* courtship sound. The strong response of *M. cassini* is again understandable, because such a transient contains sound frequencies overlapping those of the *M.cassini* songs.

There is no significant difference in the latency of the auditory nerve responses in the two species when stimulated with conspecific and allospecific courtship ticks, as shown by the histograms in Fig. 4. In *M.septendecim* the mean latency to conspecific sounds was 20.4 SD ± 0.8 ms, and to allospecific sounds was 20.7 ± 0.8 ms. In *M.cassini* the values were 19.7 ± 2.8 ms (conspecific) and 18.7 ± 3.7 ms

(allospecific). Such a result would be expected if the latency is mainly determined by the rise time of the sound.

Okanagana rimosa also emphasizes the importance of the sound frequency in its auditory nerve response. When stimulated with the courtship sounds of *M.septendecim* (Fig. 5, 1, upper trace) and of *M.cassini* (Fig. 5, 2, upper trace) auditory receptors are excited. However, the compound response is considerably stronger to *M.cassini* courtship ticks (Fig. 5, 2, lower trace), the sound spectrum of which overlaps that of the *O.rimosa* calling and courtship songs (Table 1). The much weaker response to *M.septendecim* courtship sounds (Fig. 5, 1, lower trace) can again be explained by the lack of sound frequency

O. rimosa   75 dB
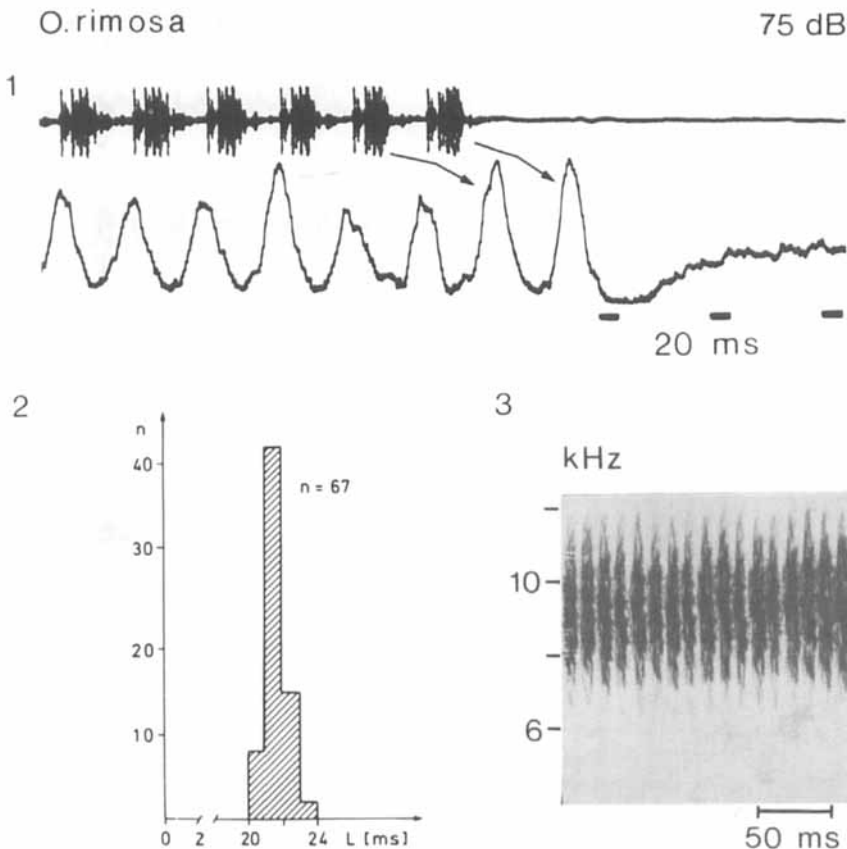
FIG. 6. 1. Auditory nerve responses (lower trace) of an *O.rimosa* female to six consecutive double pulses (combined close alternations of both tymbals) seen in the upper trace. Conspecific calling song is presented at 75 dB SPL. Arrows show the relationship of the compound auditory nerve potentials to corresponding double pulses. 2. Latency histogram ($n = 67$ = no. of double pulses) of the auditory compound action potentials (shown in 1). 3. Sound spectrogram of a part of the conspecific calling song with 17 double sound pulses; frequency range, 7–11 kHz.

3

overlap between the two species. However, as soon as short transients with broad frequency bands are used as stimuli (arrows in Fig. 5, 1) the response is strongly increased and resembles that shown in Fig. 5, 2.

Temporal structure of the song and auditory nerve response

As already shown in Figs. 2–5, the compound auditory nerve response 'copies' the rhythm of buzzes and ticks, if those are presented within the appropriate frequency range. In all four species each single tymbal

muscle contraction produces a sound pulse (Table 1) composed of a short train of sound bursts. The number of bursts is determined by the number of tymbal ribs being activated (Moore & Sawyer, 1966; Moore & Kausch, 1975). The individual sound bursts, each resulting from a single tymbal rib in-movement, are not copied in the summed auditory nerve activity, although there is an indication in some recordings that single auditory receptors or groups of receptors may even follow the rate of individual rib in-movements. However, the rate of sound pulses, each resulting from a tymbal action (i.e. single tymbal muscle
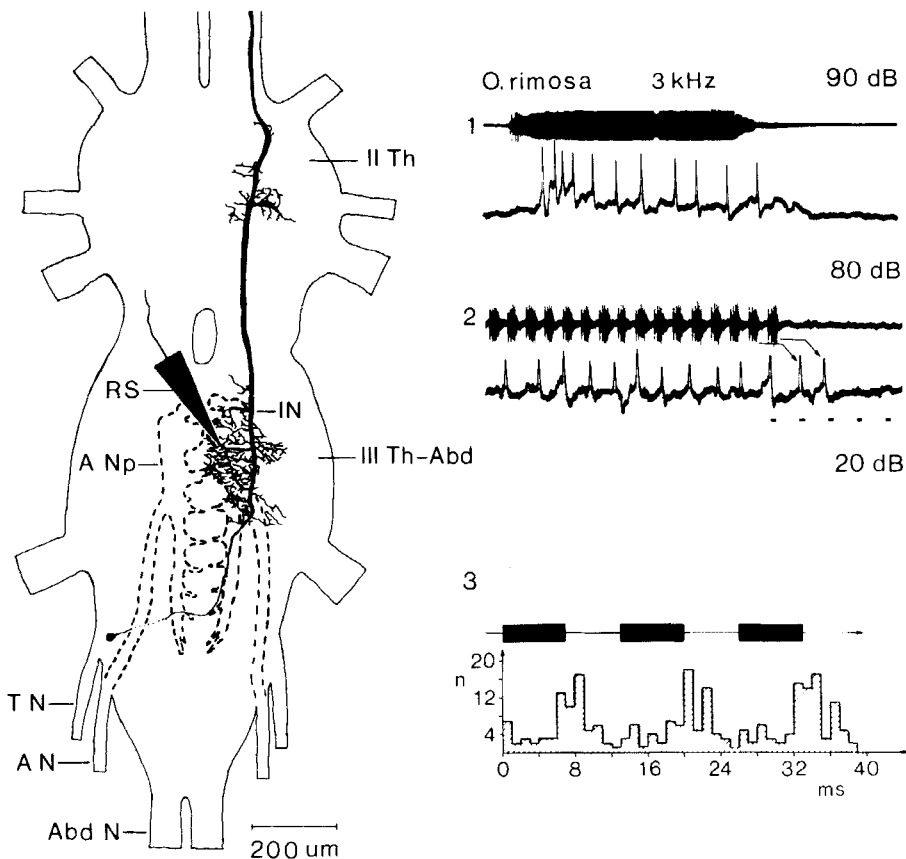

FIG. 7. Sketch of the mesothoracic (II Th) and the metathoracic–abdominal ganglionic complex (III Th–Abd) of female *O.rimosa* showing the auditory neuropiles (dashed lines, ANp) of both sides and an ascending interneurone (IN; from a camera lucida drawing) with arborizations in the meso- and metathoracic ganglia; RS, microelectrode recording site in a branch which runs medially; other details as in Fig. 1. Right, intracellularly recorded responses to a 3-kHz tone pulse at 90 dB SPL (1), and to the conspecific calling song presented at 80 dB SPL (2); arrows show the relationship of interneuronal spikes to corresponding sound pulses. 3, upper, three consecutive sound pulses (double pulses, schematized) of *O.rimosa* calling song drawn to correct time scale; 3, lower, occurrences (n) of spikes per unit time relative to the onset of the previous three sound pulses within a continuous *O.rimosa* calling song. The neurone is modulated by the sound pattern.

contraction) is copied by the summed auditory nerve response, as shown in Fig. 6 (1, lower trace). Each pulse gives rise to one compound action potential. The latencies vary between 20 and 23 ms in the case of *O.rimosa* (Fig. 6, 2: mean 21.2 SD ± 0.6 ms). Furthermore, a rather stable phase relationship exists between sound pulse and the corresponding compound action potential. Artificial and short sound pulses in the best frequency range of the species were followed up to rates of 200/s which cover the natural range.

Intracellular recording from an identified interneurone

From the metathoracic ganglion intracellular recordings were made from interneurones responding to acoustic stimuli. Two recordings were obtained from *M.septendecim*, four from *M.cassini*, and six from *O.rimosa*. However, an interneuron (*O.rimosa* female) was stained in only one case and its structure was not completely revealed. The characterization, therefore, is mainly based on a physiological comparison of interneuronal responses studied in two *Magicicada* and one *Okanagana* species.

Morphological features. One successful intracellular staining was obtained in a female *O.rimosa* (Fig. 7, left). In this case the micropipette filled with a 30% cobalt nitrate solution penetrated one of the larger branches running toward the midline within the metathoracic ganglion (RS in Fig. 7). The interneurone has a cell body in the abdominal part of the ganglionic complex which is situated contralateral to the course of the ascending axon. A zone of arborization with medially and laterally oriented branches is limited to the metathoracic part of the ganglionic complex, and overlaps the anterior region of the sensory neuropile formed by elements of the auditory nerve (dashed line, Fig. 7; Wohlers *et al.*, 1979). The axon, with a maximum diameter of 20 μm, runs forward to the meso- and prothoracic ganglia, and probably further. Within the mesothoracic ganglion the interneurone branches medially and laterally to regions of dorsal (motor?) neuropile.

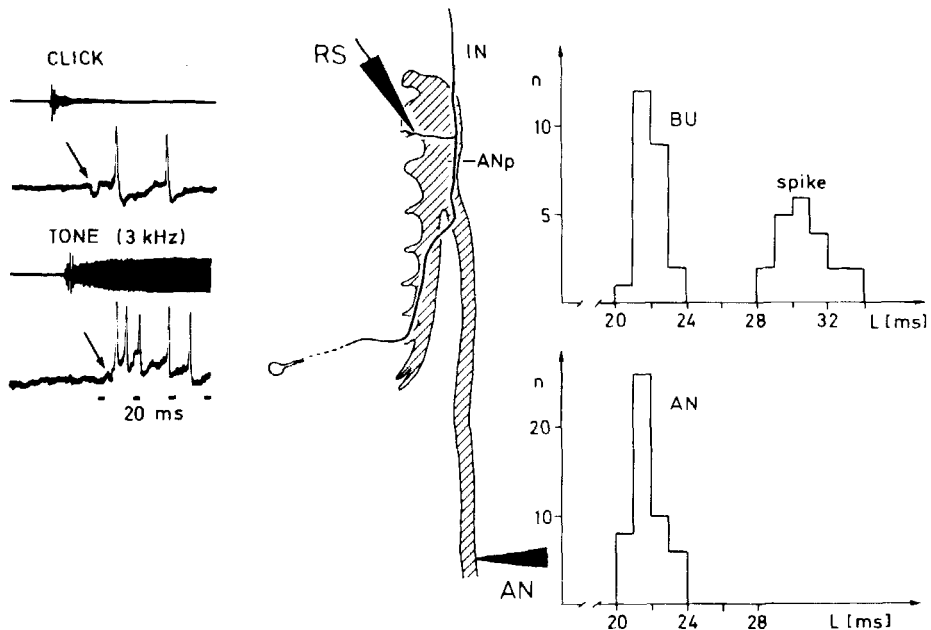*Physiological features.* The morphologically

FIG. 8. Left, interneurone responses of *O.rimosa* female (same neurone as in Fig. 7) to click and tone. Arrows point to bumps. Centre, schematic drawing of one auditory neuropile (ANp) and of a part of the ascending interneurone (IN) shown in detail in Fig. 7; RS, recording site. Right, latency histograms of the responses in the auditory nerve close to its entrance into the ganglionic complex (lower graph, AN), and of the responses in the interneurone (upper graph) separated for bumps (BU) and spikes (spike).

identified interneurone of *O.rimosa* female responded to clicks, tones (Fig. 7, 1) and to conspecific calling and courtship songs (Fig. 7, 2). Other songs could not be tested, because intracellular recordings with cobalt-electrodes did not usually last longer than 15 min (see Wohlers & Huber, 1978). The spike response to the conspecific calling and courtship songs was frequently phase-locked to sound pulses originating from double tymbal actions (Fig. 7, 3), though a single sound pulse did not always evoke a spike in the interneurone. Nevertheless, it is justifiable to conclude that the temporal pattern of pulses in the song, perfectly copied by the auditory nerve response (see Fig. 6, 1), also modulates the spike discharge in this ascending auditory interneurone.

As seen from intracellular responses to clicks and tones (Fig. 8, left), and natural songs (not shown in the figure) the spike train evoked in the interneurone is preceded by a bump of small amplitude and opposite polarity (arrows). We interpret this bump to be the reflection of an arriving afferent volley at the region of the microelectrode, an interpretation supported by latency measurements. Latencies for auditory nerve responses, recorded near the entrance to the ganglion and 0.6 mm away from the intracellular recording site (AN in Fig. 8) cover 20–23 ms (mean 21.3 SD ± 0.8 ms). At comparable sound intensities (80–90 dB SPL) these latencies are very similar to those of the bumps seen at the interneurone recording site (RS in Fig. 8: range of latencies 20–23 ms; mean 21.5 ± 0.7 ms). Therefore, the possibility of direct transmission from auditory afferents to the interneurone cannot be excluded. In the preparation shown in Figs. 7 and 8, spike latencies were several ms longer, indicating that the electrode was closer to the synaptic region than to the spike-generating
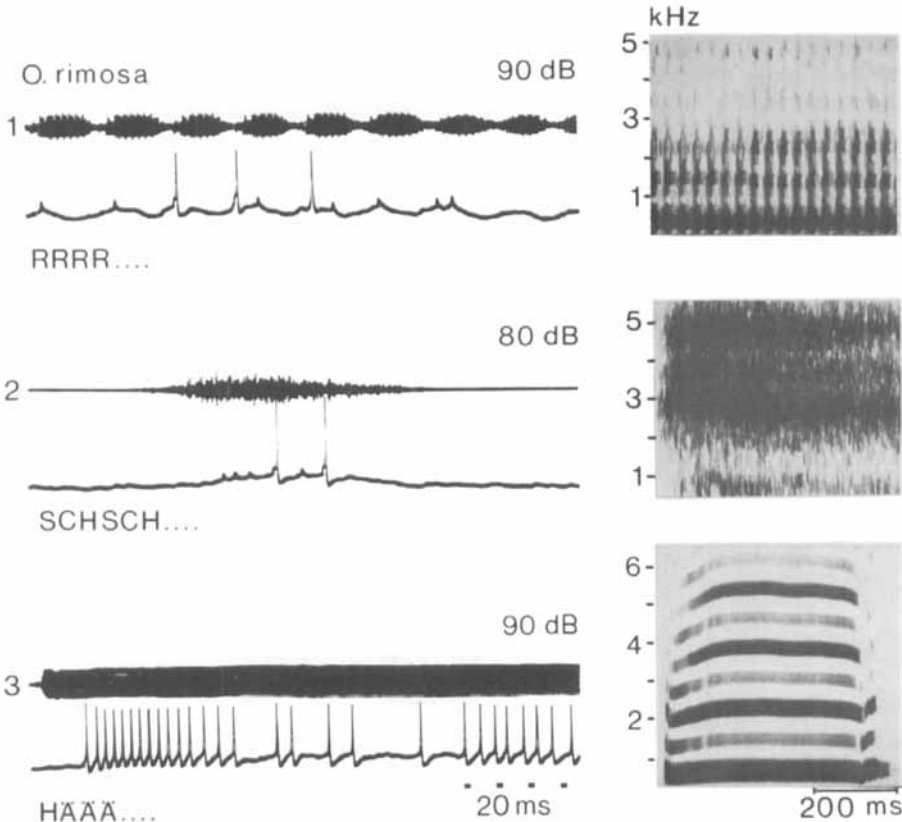

FIG. 9. Left, intracellularly recorded interneurone responses of an *O.rimosa* female (lower traces in 1–3) to three types of sounds produced by human mouth (upper traces in 1–3) presented at 80 and 90 dB SPL. Right, corresponding sound spectrograms.

zone. The close neighbourhood to the synaptic input region is also indicated by the strong sub-threshold activity of the interneurone.

Interneuronal responses to artificial sounds. Okanagana rimosa, and also 17-year cicadas, live in habitats where noises created by the wind, bird songs, sounds of other insect species, etc., are frequently heard. Birds in particular are known to hunt for cicadas. For the prey it would certainly be advantageous to extend the auditory range into the frequency bands used by possible predators. Fig. 9 shows responses of an interneurone in an *O.rimosa* female to artificial sounds produced by the human voice which were rough imitations of noises heard in the habitat of *O.rimosa*. None of the noises covered the best frequency

range (Table 1) but parts of the sound spectra overlapped with those of *O.rimosa* songs. 'RRRR...' sounds, characterized by a sequence of 'pulses' repeated at a rate of approximately 30 Hz, elicited rhythmical fluctuations of the membrane potential, EPSPs and spikes, the latter being phase-locked to the pulses (Fig. 9, 1). 'SCHSCH...' noises depolarized the cell, EPSPs were generated and sometimes led to a spike (Fig. 9, 2). The best spike response was achieved by the imitation of a bird cry (Fig. 9, 3).

Specificity of the interneurone response in sympatric species

One of the best examples for species-specificity within the auditory pathway of an

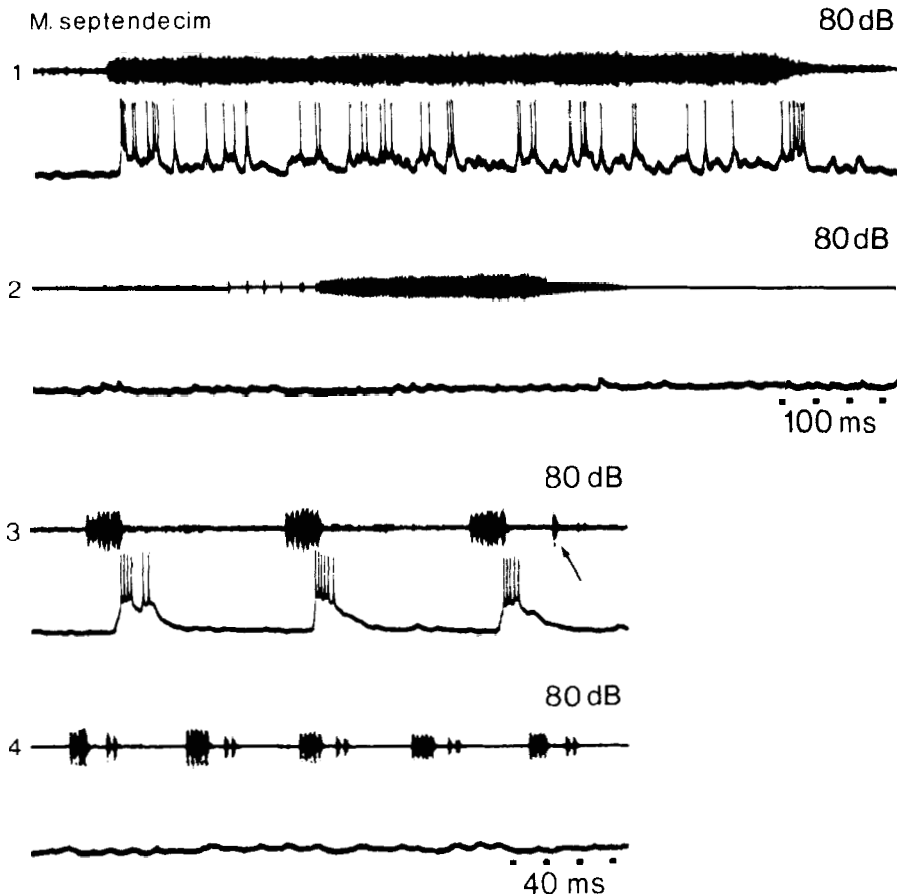

FIG. 10. Interneurone responses (recorded intracellularly) from a female *M.septendecim* (lower traces in 1–4) to conspecific calling and courtship songs (upper traces in 1 and 3, respectively), and to allo-specific *M.cassini* calling and courtship songs (upper traces in 2 and 4, respectively). Arrow in 3 points to single sound burst within a *M.septendecim* buzz which elicited no response. Stimulus intensities 80 dB SPL.

insect is shown in the response of an inter-
neurone from a *M.septendecim* female (Fig.
10). In the whole intensity range tested,
conspecific calling and courtship songs caused
a distinct depolarization and spike discharge
(Fig. 10, 1 and 3), whereas there was an entire
lack of spike response to the songs of *M.
cassini* (Fig. 10, 2 and 4). As far as the calling
songs of the two species are concerned, the
auditory nerve of *M.septendecim* acts as a
filter, as already noted (Fig. 3, 1 and 2, left
column), and there seems to be little input to
the ganglion generated by the *M.cassini* call.
However, and as indicated in Fig. 4 (2, left
column), the auditory nerve of *M.septendecim*
exhibits compound action potentials even in
response to *M.cassini* courtship ticks at
comparable intensities; therefore, the inter-
neurone should receive auditory input. The
complete absence of spikes, and the reduced
sub-threshold activity (Fig. 10, 2 and 4) must
result from an additional filter acting between
the auditory nerve input and the spike output
of the interneurone.

M.cassini interneuronal responses also point
to species-specificity (Fig. 11). Again the
strong response to the conspecific calling song
is striking, and in particular the high degree to
which the temporal pattern is copied by the
neurone both in sub-threshold (synaptic) and
spike activity (Fig. 11, 2). The call of *M.
septendecim*, even when presented at 10 dB
higher intensity, elicited only a small increase
if any in the spontaneous firing rate (Fig. 11,
1). Less striking, but nevertheless clearly visible,
is the difference in response to conspecific
and allospecific courtship sounds (Fig. 11, 3
and 4). The conspecific courtship sound
elicited more spikes (imp.) per tick (Fig. 11,
histograms lower right), and the temporal
structure of the song was copied in great
detail (Fig. 11, 4). A comparison of the
strength of response in terms of numbers
of spikes per *M.cassini* courtship tick (duration
20 ms) shows a statistically significant
difference (Fig. 11, lower right, right histo-
gram), with the mean response to *M.cassini*
(conspecific song) at 4.4 ± 0.5 spikes (imp.)/
20 ms and to *M.septendecim* (allospecific
song) 2.9 ± 0.6 spikes (imp.)/20 ms. There is
a strong response of the *M.cassini* inter-
neurone to sharp transients (Fig. 11, 3, arrow)
which contain a much broader frequency

band than the *M.septendecim* courtship
buzzes (Table 1).

As shown in Fig. 12 (1) the spontaneously
active interneurone of an *O.rimosa* female
appears to be unaffected in its firing rate by
the call of *M.septendecim* (Fig. 12, 1: mean
interspike interval for the spontaneous dis-
charge 42.1 SD ± 15 ms, for the discharge
during the call 43.4 SD ± 21 ms). However,
when stimulated with the call of *M.cassini*
(Fig. 12, 2) the interneurone increased its
firing rate during the buzz-part. Within the
preceding series of ticks (Table 1) a grouping
of spikes is recognizable. Also, *M.septendecula*
calls modulated the spontaneous firing rate
(Fig. 12, 3) and the neurone copied ticks and
buzzes. Again, the complete absence of a
response to the *M.septendecim* call, and the
modulating effect of the *M.cassini* and *M.
septendecula* calls upon the *O.rimosa* inter-
neuronal discharge can be explained by the
differences in sound frequency spectra (see
Table 1) and the overlap with *O.rimosa*
songs.

A similar difference in the sound frequency
spectra (Fig. 4) is responsible for the observa-
tion that *M.septendecim* courtship buzzes
elicited much weaker or even nil responses in
the *O.rimosa* interneurone, whereas *M.cassini*
courtship ticks greatly modulated and timed
the neurone's spontaneous discharge (Fig. 12,
4 and 5). The difference in response strength
is statistically significant (Fig. 12, histogram
lower right; mean for the courtship buzz
stimulus of *M.septendecim* 0.8 SD ± 0.7 spikes
(imp.)/tick ($n = 57$), and for the courtship
tick of *M.cassini* 2.7 ± 0.7 spikes (imp.)/tick
($n = 57$)). Sharper transients, indicated by
arrows in the *M.septendecim* courtship song
(Fig. 12, 4), with a much broader frequency
band led to a stronger *O.rimosa* interneuronal
response.

Species-specificity in the *M.septendecim*
and *M.cassini* interneuronal responses to
natural conspecific and allospecific calling and
courtship song appears to be primarily based
on the frequency tuning of the hearing organs
to the characteristic bands of the species
song. However, there must exist additional
filter properties within central parts of the
auditory pathway to account for the inter-
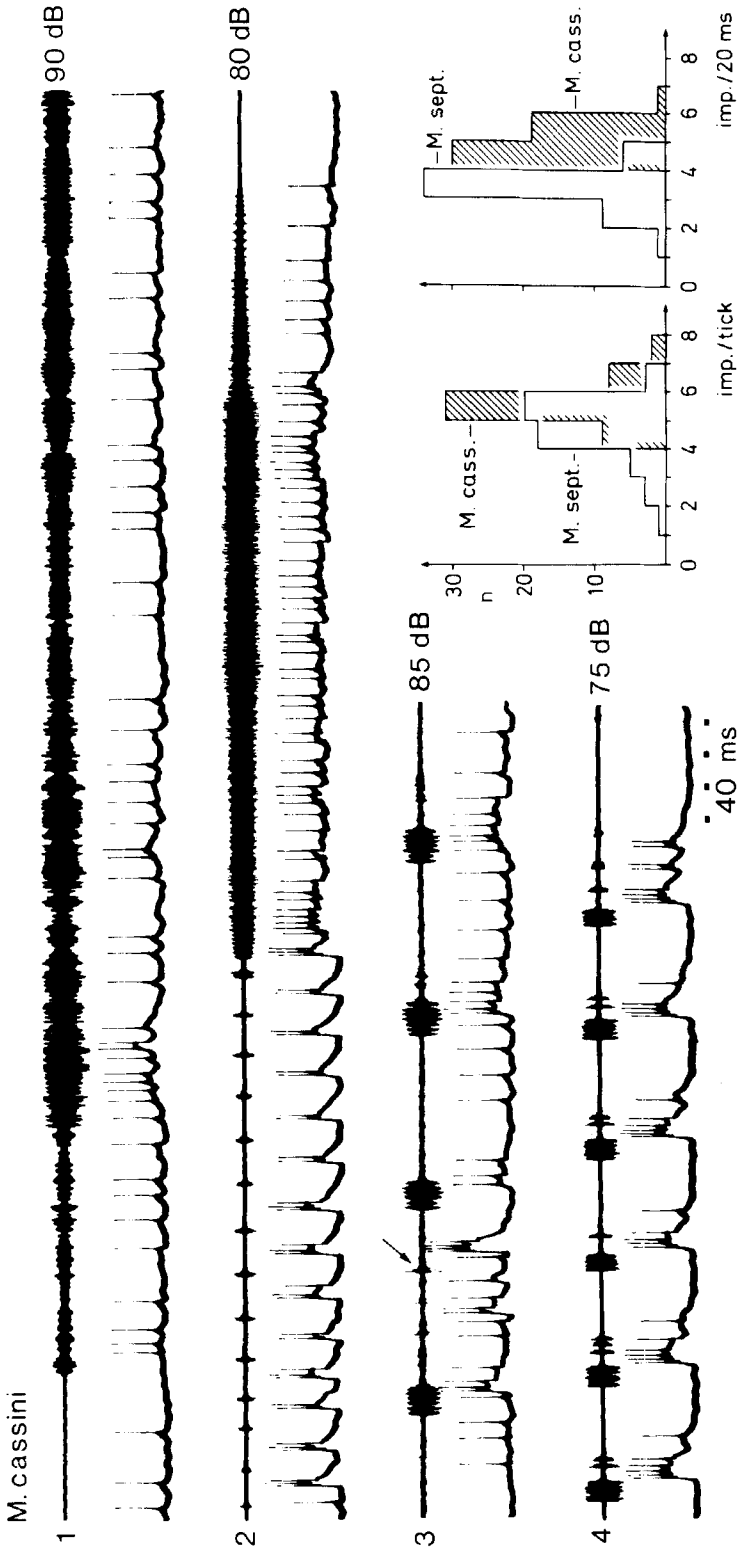neurone's specificity in the frequency
domain.

FIG. 11. Interneurone responses (recorded intracellularly) from a female *M.cassini* (lower traces in 1—4) to calling and courtship songs (upper traces: *M.septendecim*, 1 and 3; *M.cassini*, 2 and 4). Stimulus intensities are 75, 80, 85 and 90 dB SPL. Arrow points to sharp transient and to the strong interneuronal response. Lower right, histograms of the interneurone responses of *M.cassini* in terms of spikes (imp.) per courtship buzz of *M.septendecim* and per courtship tick of *M.cassini* (left histogram). Right histogram shows the response per 20 ms (imp./20 ms). 20 ms were chosen because they represent the average duration of the first tick in each *M.cassini* double courtship tick (Table 1) while *M.septendecim* courtship buzzes are usually twice as long.
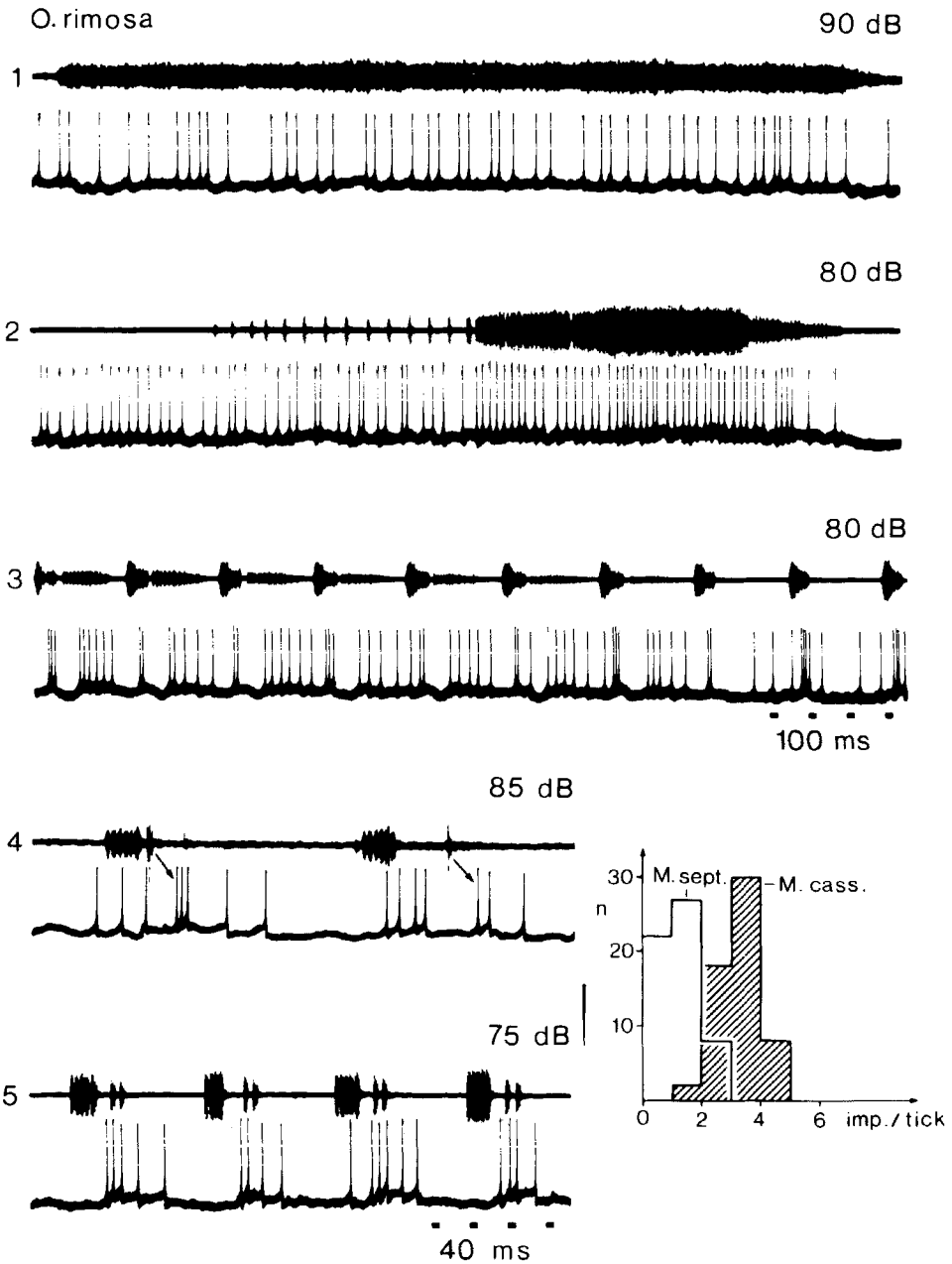
FIG. 12. Interneurone responses (lower traces in 1–5) of an *O.rimosa* female to calling (1–3) and courtship songs (4 and 5) of 17-year cicadas presented at intensities of 75, 80, 85 and 90 dB SPL. 1 and 4, *M.septendecim* songs; 2 and 5, *M.cassini* songs; 3, *M.septendecula* call (transition from the tick-buzz part to the tick). Arrows in 4 relate sharp transients in the *M.septendecim* courtship song (apparently sounds caused by wing flipping) to stronger interneuronal responses. Lower right, histograms summarizing the spike responses, plotted as the number (n) of spikes per tick (or short buzz) to *M.septendecim* and *M.cassini* courtship songs.

Discussion

The investigation of sound communication behaviour in the field and within the laboratory, combined with studies of the structure and the function of sensory and neuronal elements composing the auditory pathway in insects, should eventually give some insight into the mechanisms governing sound reception, species discrimination, and species recognition. So far most of the work has been done on orthopterans; therefore it seems necessary to discuss present findings from a comparative standpoint.

Behavioural aspects

In gryllids, tettigonids and many cicadas, the males sing and the females respond phonotactically. In acridids, and some cicadas, both males and females stridulate and approach each other (Dumortier, 1963; Leston & Pringle, 1963; Moore, 1973). Species-specific sound parameters have been described for all four groups of singing insects (see Alexander, 1960, 1975); however, behavioural experiments designed to analyse intraspecific sound recognition are rare. For crickets this has been done by Regen (1913, 1923), Walker (1957), Murphey & Zaretsky (1972), Zaretsky (1972), Ulagaraj & Walker (1973, 1975), Popov *et al.* (1974), Hill (1974), Popov & Shuvalow (1977), Hoy *et al.* (1977) and Moiseff *et al.* (1978); for acridids by Loher (1957), von Helversen (1972) and von Helversen, D. & O. (1975). The studies of phonotaxis in gryllids and of sound responses in acridids have shown that the carrier frequency and the temporal patterns of the songs are the most significant behaviourally (see Elsner & Huber, 1973; Elsner & Popov, 1978). Therefore, the sensory and neuronal machinery which evolved in the context of processing sound signals must be suited to differentiate among these features. Unfortunately for cicadas, even for those species in which the songs are described in detail, very few quantitative behavioural studies have been performed (Alexander & Moore, 1958). This is partly because of their long life cycles, short adult periods, daily activities, and difficulties with their food requirements. However, such studies are urgently needed, because they

provide the platform for physiological investigations in sound communication.

Auditory nerve and species demands

In orthopterans, pitch discrimination is accomplished through the biophysical properties of the hearing organs which provide the basis for tuning of auditory receptors to different frequencies, paralleling the species' signals. Temporal features of the songs are copied in the spike discharge pattern of auditory sense cells (for crickets see Nocke (1972), Zhantiev & Tshukanov (1972a, b), Hill (1974), Eibl & Huber (1979) and Esch *et al.* (1980); for tettigonids see Zhantiev (1971), Rheinlaender (1975), Kalmring *et al.* (1978a) and Zhantiev & Korsunovskaya (1978); for acridids see Michelsen (1966, 1971).

In cicadas less information is available and it is based only on auditory nerve recordings (see Introduction). *M.septendecim* songs are emitted in a frequency range which does not overlap those of the two other sympatric species, and its hearing organs appear sharply tuned to the intraspecific frequency bands (Simmons *et al.*, 1971). This tuning may explain the powerful response in the auditory nerve to the conspecific call, and the failure to respond to allospecific songs, as shown in this paper. However, the parameter 'sound frequency' alone does not guarantee the acoustical separation of the three 17-year cicada species. For instance, the frequency spectra from the songs of *M.cassini* and *M. septendecula* overlap to a large degree, resulting in auditory nerve responses to songs of both species. But in these two species, interspecific separation may be improved through differences in the temporal organization of the song (Table 1) and in diel separation of singing periods (see Alexander & Moore, 1958, 1962). In addition, the courtship songs of all three species contain buzzes and ticks with sharp transients, and they are not separated at the level of the hearing organs (Figs. 4 and 5).

The structure and operation of the sound-producing apparatus enables cicadas to emit sound with sharp transients (Pringle, 1954; Moore & Sawyer, 1966; Popov, 1975; Simmons & Young, 1978). The hearing organs are

adjusted to respond to such transients, as shown for Sri Lankan cicadas (Pringle, 1954), for a Brazilian cicada (Enger *et al.*, 1969), and for North American species (this paper). The response seems to be best if the transients contain that frequency range to which the hearing organ is tuned, as strongly indicated in this paper.

All species studied here produce sounds only as each tymbal buckles inward, and are effectively silent during outward tymbal movement. In those species where the tymbals operate nearly continuously, repetition rates of 80–100 Hz are reached by each tymbal. Since the tymbals are driven alternately (see Hagiwara & Watanabe, 1956; Moore & Sawyer, 1966; Reid, 1971; Simmons & Young, 1978) the total tymbal repetition rate is doubled and reaches values of up to 200 Hz. Auditory sense cells are adjusted to such rates, and no adaptation is seen (Enger *et al.*, 1969; and above). In all tymballing species, the tymbal is subdivided into ribs, and each rib causes a separate burst of sound. Such rib-bursts reach rates of 600–1000 Hz (Moore & Sawyer, 1966) and together comprise the sound pulse from each tymbal. It is doubtful whether single auditory sense cells can resolve these rib-rates, although auditory nerve discharges from *O.rimosa* frequently show a rough outline of the substructure within a paired tymbal action (Fig. 6, 1).

Auditory interneurones and species demands

In orthopterans, the tuning of segmental and plurisegmental ascending and descending interneurones has been described together with how they copy the temporal structure of natural and artificial sounds (see Elsner & Popov, 1978; and for recent data, Boyan, 1978, 1979b; Hoy, 1978; Kalmring *et al.*, 1978a,b; Popov *et al.*, 1978; Wohlers & Huber, 1978; Stout & Huber, in preparation).

In crickets, location of the sound source in space, which is partly due to the physical properties of the accessory structures of the hearing organs (Paton *et al.*, 1977; Hill & Boyan, 1977; Larsen & Michelsen, 1978; Boyan, 1979a,b; Kleindienst *et al.*, in preparation), is greatly improved by mutual inhibitory interactions via segmental interneurones (Wohlers & Huber, 1978) and by the

spread of this inhibitory influence to ascending auditory neurones (Wiese, personal communication). For cicadas, directional hearing has been shown in *Cystosoma saundersii* (Young & Hill, 1977), but information at the interneuronal level is still lacking.

The processes underlying sound recognition begin at the level of the hearing organs and continue within the auditory pathway (see Elsner & Popov, 1978; Huber, 1978). In orthopterans, ascending auditory neurones do not always exhibit a sharper tuning to sound frequencies than do primary auditory fibres (Popov, 1973; Kalmring, 1975; Rheinlaender, 1975; Rheinlaender *et al.*, 1976, Stout & Huber, in preparation). This means that species recognition in the sound frequency domain is mainly accomplished at the level of the sensory system.

For cicadas, quantitative information is still lacking, but there is good evidence, at least for *M.septendecim* and *M.cassini* that ascending interneurones cover approximately the same frequency range as the hearing organs. This is indicated by the strong response of the *M.septendecim* interneurone to conspecific calling and courtship songs, and the complete lack of response to *M.cassini* songs. However, there seem to be differences between cicada species, particularly as far as the courtship songs are concerned, where species-specificity is less pronounced. Finally, the interneurones recorded in *O.rimosa* females can be excited by tones outside the species song frequency range (Fig. 7), and they may thus serve other functions.

In the temporal domain, orthopterans possess ascending interneurones which copy song patterns in terms of syllables and chirps, without habituation (Stout & Huber, 1972; Huber, 1977). But there exist others with different encoding properties (Popov *et al.*, 1974; Kalmring, 1975; Rheinlaender, 1975). The interneurones recorded from *M.septendecim* and *M.cassini* cicadas seem to belong to the type of the non-habituating units which encode buzzes and ticks, the rhythm elements of cicada songs. They can be considered as part of the sound recognizing system within the CNS.

There are field observations from Alexander & Moore (1958) which support our finding of a preference in copying the temporal

parameters of the conspecific calling songs of *M.septendecim* and *M.cassini*. In field behavioural analyses of tape-recorded sounds of *M.cassini* males, Alexander & Moore found that hearing only the beginning of the buzz part of their calling song stimulated buzzing in the males, while hearing the whole buzz or a suddenly interrupted buzz stimulated ticking within about half a second. Hearing only the ticking part of the call commonly caused males to buzz. Furthermore, males of *M.cassini* also sang more often when hearing their calling songs, but not when hearing their court-ship sounds. There was no increase in singing when hearing the calling songs of *M.septendecim*.

Acknowledgments

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