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The function of auditory neurons in cricket phonotaxis

II. Modulation of auditory responses during locomotion

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Summary. The activity of auditory receptor cells and prothoracic auditory neurons of the cricket, *Gryllus bimaculatus,* was recorded intracellularly while the animal walked on a sphere or while passive movement was imposed on a foreleg.

During walking the responses to simulated calling song is altered since (i) the auditory sensory cells and interneurons discharged impulses in the absence of sound stimuli (Figs. 1, 3) and (ii) the number of action potentials in response to sound is reduced in interneurons (Figs. 2, 3).

These two effects occurred in different phases of the leg movement during walking and therefore masked, suppressed or did not affect the responses to auditory stimuli (Figs. 3, 4). Hence there is a time window within which the calling song can be detected during walking (Fig. 5).

The extra excitation of receptors and interneurons is probably produced by vibration of the tympanum because (i) the excitation occurred at the same time as the leg placement (Fig. 4), (ii) during walking on only middle and hindlegs, no extra action potentials were observed (Fig. 6), (iii) in certain phases of passive movements receptor cells and interneurons were excited as long as the ipsilateral ear was not blocked (Figs. 8, 9).

Suppression of auditory responses seems to be peripheral as well as central in origin because (i) it occurred at particular phases during active and passive leg movements in receptor cells and interneurons (Figs. 1, 4, 9), (ii) it disappeared if the ear was blocked during passive leg movements (Fig. 9) and (iii) it persisted if the animal walked only on the middle and hind legs (Fig. 6).

Introduction

The preceding paper (Schildberger and Hörner 1988) was concerned with the specific roles of identified prothoracic auditory neurons in sound localization, and focussed on their effects on phonotactic walking. However, it was evident in those recordings that the auditory responses of the interneurons are, in turn, affected by locomotion. Discharges strongly correlated with the song syllables were observed only when the animal was standing still; during walking, the number of action potentials uncorrelated with the stimulus increased, and some action potentials that would otherwise have appeared in response to the song were absent. Whether by peripheral and/or central processes, walking influences hearing.

Modulation of the activity in sensory pathways during locomotion is a common phenomenon and has been studied in various sensory systems and behaviors in vertebrates and invertebrates. The modulation can be both peripheral and central in origin (Russel and Roberts 1974; Heitler 1983; Krasne and Bryan 1973; Murphey and Palka 1974; Daley and Delcomyn 1980; Kämper and Dambach 1981; Orida and Josephson 1978). Auditory neuron activity in orthopteran insects is modulated during stridulation and flight (Boyan 1986; Hedwig 1986; Wolf and von Helversen 1986; Tomioka and Yamaguchi 1984).

Here we examine the way in which the responses of auditory neurons of crickets to sound are affected by walking, the temporal relations between modulation of the response and the phase of leg movement, and whether the modulation originates in the auditory organ itself or in central nervous processes.

Materials and methods

Female crickets of the species *Gryllus bimaculatus* aged 2–4 weeks (following the imaginal moult), taken from the laboratory colony, were mounted on a holder in such a way that they could walk on a rotatable styrofoam sphere during intra-

cellular recording. Recordings were obtained from a total of 46 identified auditory interneurons in the prothoracic ganglion and from the axons of 12 auditory receptor cells. Preparation and mounting of the animals and the methods of stimulation, recording, identifying the neuron type and data analysis were identical to those described in the previous paper (Schildberger and Hörner 1988). In addition, the activity of the trochanter levator muscles (M76; see Laurent and Richard 1986) in the forelegs was monitored with copper-wire electrodes implanted in the coxa. The movement of a foreleg was recorded either with a photodiode aimed at the femur from above or with a capacitive probe (DISA 51E01). The probe was set up 0.5 cm beyond the extreme anterior position of the foreleg. Because the extreme posterior position of the leg was outside the linear range of the probe and the leg moves in three dimensions during a step, the output signal from the probe did not reflect the actual movement of the leg. But it did indicate fairly accurately the extreme anterior position, because here the probe operates linearly and the leg motion reverses sharply at this position (end of swinging phase, placement of the leg and beginning of the pushing phase).

For the experiments with passive leg movement the animal was mounted with the dorsal surface down (Fig. 9), the ventral surface was removed to expose the prothoracic ganglion, and a glass microelectrode was inserted into the ganglion. Sound stimuli were presented via a loudspeaker set up in front of the animal. Passive movement of the leg was produced by a metal ring slipped onto the distal part of the tibia so that it could slide freely over the tibial surface while being driven back and forth with a d.c. motor so as to rotate the tibia about the femur/tibia joint as shown in Fig. 9. The angle covered by this movement was constant, 60°, one back and forth period lasted 1.2 s, and the velocity of movement varied sinusoidally. The direction of movement was recorded with a photodiode. Conventional methods were used to record the neuronal responses and examine histologically the cells marked intracellularly with Lucifer Yellow.

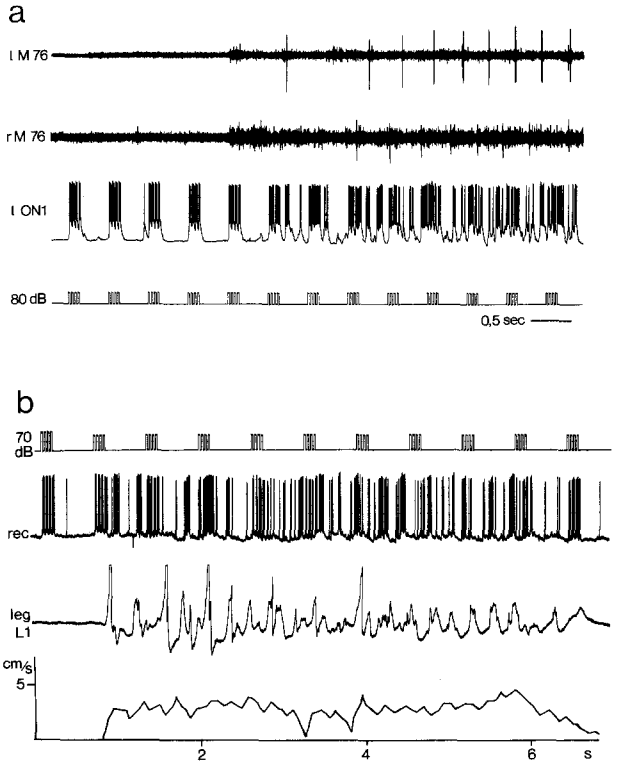

Fig. 1. a Activity of the left (top) and right (2nd trace) trochanter levator muscle (*M76*) and of the left ON1 (3rd trace) during presentation of artificial calling song (bottom). The activity of ON1 in response to the first 5 chirps, while the animal was standing still, is distinctly different from that during subsequent walking. **b** Recording from an auditory receptor cell (2nd trace) in the left ear during walking in the presence of artificial calling song; third trace shows the movement of the left foreleg as measured with a photodiode, and the fourth is a record of walking velocity. The activity of the receptor cell is also modulated during walking

Results

Responses to artificial calling song

The responses of auditory neurons and receptors in a tethered cricket that is standing still closely resembled those measured in an animal fixed by the dorsal surface (see Wohlers and Huber 1982; Oldfield et al. 1986). The neurons had little or no resting activity. Their thresholds to 5 kHz tones were about 15 dB higher when the sound was contralateral than when it was ipsilateral; the threshold of the omega neuron ON1 was 45–50 dB, that of the ascending neuron AN1 40–45 dB, and that of the ascending neuron AN2 50–55 dB. Receptors, ON1 and AN1 copied the temporal pattern of the chirp in their discharge.

But the activity of all the interneurons studied changed when the animal was walking, and so did that of the auditory receptors (Fig. 1). Most examples shown are from ON1, but the effects have been observed in AN1 and AN2 as well. The number of action potentials uncorrelated with the sound stimulus increased, the membrane potential of the interneurons sometimes reached levels below the resting potential found in a standing animal, and in both interneurons and receptors gaps appeared in the train of impulses discharged in response to a sound stimulus. Because of these effects, the stimulus pattern was often not discernible at first glance in the discharge of the units.

When the responses of auditory interneurons to a calling song during standing are compared with those during walking, two effects are revealed (Fig. 2): First, there is a general increase in the 'background' level of excitation and hence in average discharge rate, induced by walking. Second, under otherwise identical conditions the response to the song is distinctly smaller during walking (walking-induced suppression). The response to a calling song at 60 dB is still detectable in the summed activity over several repetitions, but examination of the individual responses shows that

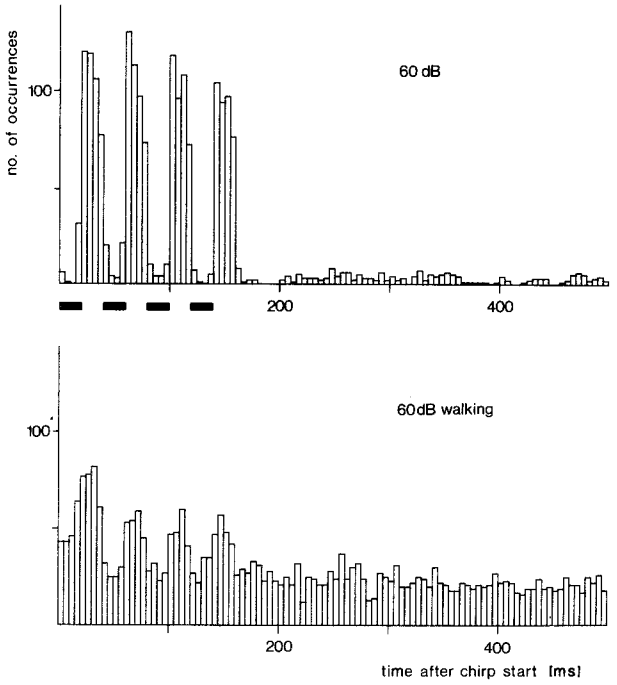

Fig. 2. PST histogram of the responses of an ON1 to ipsilateral calling song (5 kHz, 60 dB) while the cricket is standing still (top) or walking (bottom). In each histogram the responses to 180 chirps are combined; bin width 5 ms. During walking action potentials uncorrelated with the sound stimulus appear, and the response to the sound is less than during standing

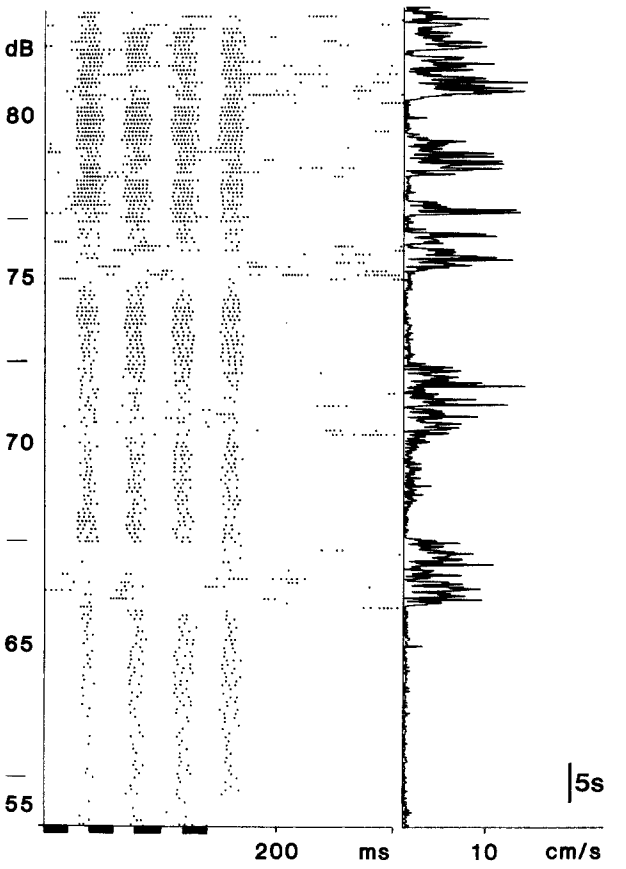

Fig. 3. Responses of AN1 to ipsilateral calling song during walking. On the left the times of occurrence of action potentials (dots) are plotted for 300 ms after the beginning of each chirp, and the responses to consecutive chirps are aligned vertically; the intensity of the chirps was increased in the indicated steps, from bottom to top. On the right is a continuous record of the animal's walking velocity during the experiment

some chirps do not elicit impulses and the response is often masked by the presence of extra impulses (Fig. 3). As the sound intensity is increased the response stands out more from this background. At 80 dB there is clear copying of the chirp pattern even during walking, although some interference is still present and the response to a syllable may fail occasionally. Both effects – walking-induced suppression and excitation – act in the same sense, to disrupt the representation of the conspecific signal.

Responses to steady tones

In order to separate the two effects noted above, a steady tone at 5 kHz was used as the auditory stimulus; the responses of the interneurons were tonic discharges (Fig. 4), so that both suppression and excitation can be discerned. There was some interneuronal activity during walking in the absence of a stimulus, and the response to a tone at 70 dB was superimposed on this walking-induced excitation (Fig. 4a). Occasionally the walking-induced suppression interrupted the tonic discharge. Walking-induced excitation and suppression are coupled to the stepping rate. If the cricket stepped more frequently, as can be seen by the increase of the frequency of muscle potentials, both effects occurred more often. Suppression effects were not necessarily tied to continuous walking; suppression can also occur during a pause in walking when the animal briefly moves a leg (Fig. 4a, arrow). Walking-induced modulation of auditory receptors and interneurons were observed in every animal, but the magnitude of the effects varied among individuals.

Auditory responses and stepping period

The correlation between the time of occurrence of the effects and the stepping period can be examined by comparing the recordings from muscle 76 (foreleg trochanter levator) with the activity of auditory neurons. During walking phasic patterns of large units and more tonic patterns of smaller units can be discerned (Figs. 1, 4). The phasic units in the muscles of the two forelegs fired in alternation dur-

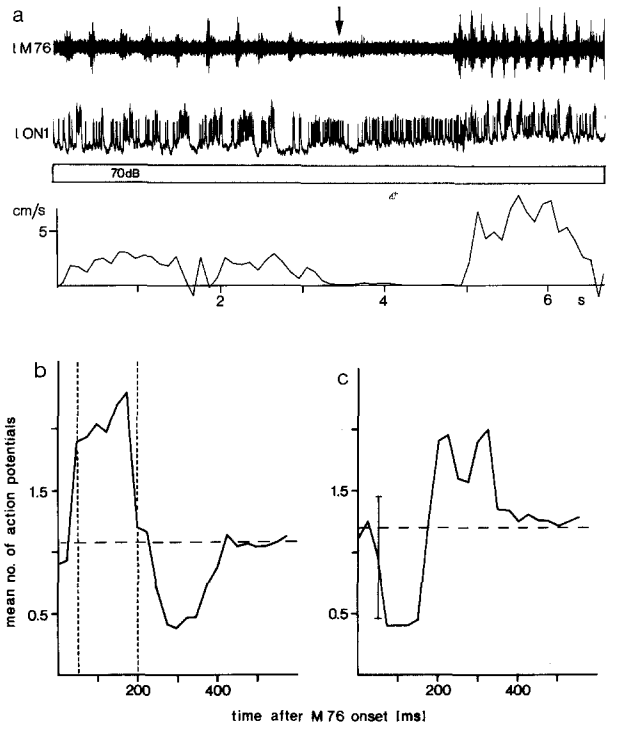

Fig. 4. a Recordings of the activity of the left trochanter levator muscle (*M76*), of the walking velocity and of the responses of the left ON1 to a steady tone while walking slowly, standing still and walking rapidly (left to right); walking is associated with occasional suppression of the response to the tone and with the addition of extra action potentials, both effects being correlated with the muscle activity; arrow marks movement of the left foreleg without walking. **b, c** Correlation between the discharge of auditory neurons during stimulation with a steady tone (5 kHz, 65 dB) and the locomotor activity. Each diagram is based on 60 stepping cycles, with periods of 350–550 ms (mean stepping period 482 ms); the beginning of the cycle (0 ms on the abscissa) coincides with the onset of the burst of activity in muscle M76. The ordinate (AP) gives the mean number of action potentials per 25 ms sample, and the horizontal dashed line shows the mean value for the response to the tone when the animal is standing still. Vertical dashed lines mark the range of delay between M76 onset and anterior extreme position of the leg. To make the short cycles comparable with longer ones, for each cycle shorter than 525 ms, this mean response value was added to each bin after the end of the cycle, up to 525 ms. The neurons represented are **b** the ON1 ipsilateral to the moving leg and **c** the contralateral ON1 in another animal

ing walking. Because the discharge of the tonic units was not precisely timed with respect to the stepping cycle the following analysis refers only to the phasic units. As the cricket walked, these phasic muscle bursts were repeated at intervals of 150–800 ms. During continuous walking the foreleg reached its extreme anterior position about 50–200 ms after the phasic burst of the muscle M76 (Fig. 4b). Stepping periods greater than about 800 ms indicated uncoordinated walking, in which the muscles on the two sides no longer operated in clear alternation, the step duration varied widely, and the walking velocity fell below 1 cm/s. Therefore only stepping periods between 150 and 600 ms were included in the following analysis of the influences on auditory responses.

The temporal relation of the response of ON1 to a steady tone (5 kHz, 65 dB) and the stepping period is illustrated in Fig. 4b, c. The extra excitation in this neuron appeared from approximately 50 to 200 ms after the muscle potential. This latency corresponded roughly to the delay between the muscle burst and the time when the ipsilateral leg reached its extreme anterior position. That is, the auditory neuron became excited when the leg was placed on the ground. Later, 200–400 ms after the muscle burst, the neuronal discharge was suppressed. Still later, the response to the steady tone reappeared. When the ON1 was contralateral to the levator muscle being considered, the relationships were reversed (Fig. 4c). Here the response was suppressed 100–200 ms after the contralateral muscle burst, and then the discharge rate rose to exceed the tonic response of the neuron. Evidently, then, at some times during the cyclic movement of the leg during walking extra excitation appeared, at others the auditory response was suppressed, and at still others the activity of the neuron was unaffected by the movement.

The consequences of these interactions for the response to the calling song are illustrated in Fig. 5. Each line of dots represents the neuronal activity from the beginning of the ipsilateral levator burst to the beginning of the burst of the next step. When the chirp started 50–200 ms after the muscle burst, the response was masked by the extra excitation. If it began 150–250 ms after the muscle burst, the response was suppressed, but there was no longer any significant effect on the response to a chirp beginning 250–400 ms after the burst. That is, there seems to be a time window at late phases of steps with long periods during which a conspecific song can be detected, even at low intensities.

Origin of the effects

A cricket can walk on four legs, with the two forelegs fixed to a holder in such a way that they do not touch the sphere and cannot bend at the joints. Under these conditions the walking velocity was distinctly lower than for six-legged walking, and there was also a clear difference in the activity of ON1 (Fig. 6). There was hardly any sign of suprathreshold excitation not coupled to the sound

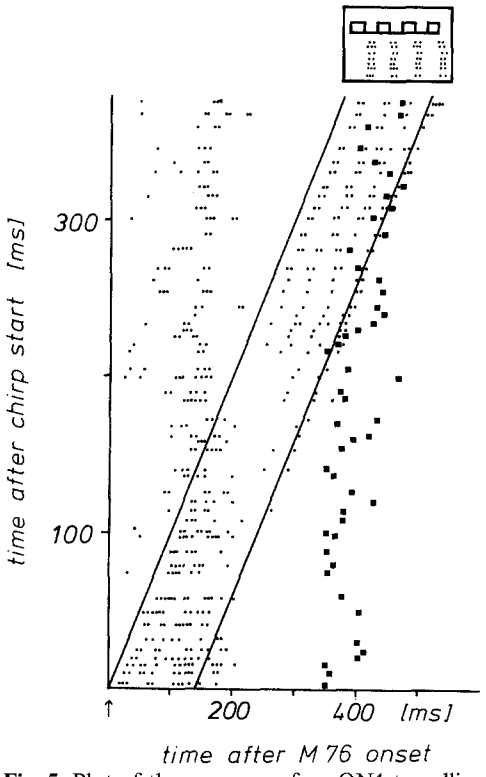

Fig. 5. Plot of the response of an ON1 to calling song (5 kHz, 65 dB) to show how modification of the response is correlated with the stepping movement. Each horizontal row of dots represents the action potentials discharged by the neuron between the beginning of a burst of activity of the ipsilateral muscle M76 (0 ms on the abscissa) and the beginning of the next muscle burst (squares). The rows are arranged vertically (from bottom to top) by the delay between the onset of the muscle burst and the beginning of the chirp. The continuous lines mark the beginning of the first syllable of the chirp, respectively the end of the last syllable of the chirp. The inset shows the response of the neuron to the calling song (marked on top, 5 kHz, 65 dB) when the animal is standing still. When the chirp begins earlier than about 200 ms after the muscle burst, additional action potentials are superimposed on the response between about 75 and 200 ms; at times between 200 and 300 ms the response is totally or partially suppressed; later than about 300 ms there is no effect on the response

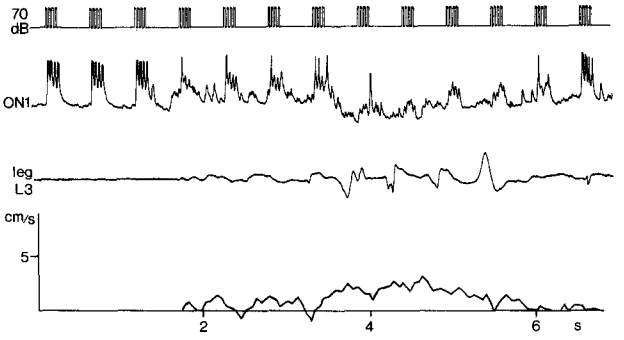

Fig. 6. Responses of the left ON1 (2nd trace) to artificial calling song (top trace) while the animal is walking on four legs, with the two forelegs fixed on a holder. Trace 3 shows the movement of the left hindleg as measured with a photodiode, and trace 4 shows the walking velocity. There is no suprathreshold extra excitation like that seen during six-legged walking, but there is a suppression of the response to sound

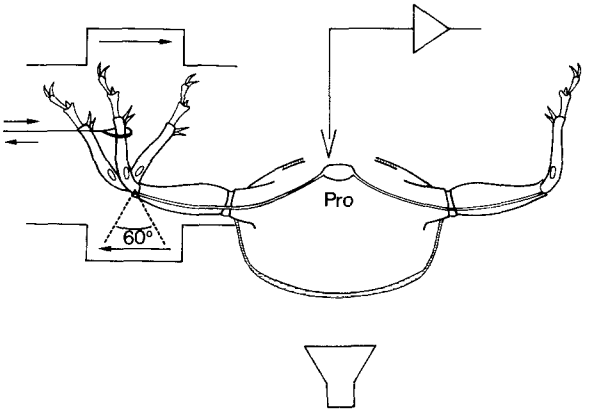

Fig. 7. Diagram to show the arrangement for intracellular recording from prothoracic auditory neurons during acoustic free-field stimulation and passive leg movement. The stimulus traces in the following figures follow the convention indicated here for direction of leg movement, thus the stimulus traces mark the occurrence and the direction of the movement but not the velocity

stimulus. However, suppression of the response to sound was still clearly discernible, and its effectiveness increases with walking velocity. This suppression is probably ascribable to central inhibition, because in this situation the foreleg cannot move. Similar effects have been observed in all ON1s ($n=4$) of animals walking on four legs.

To get a better idea of the mechanisms of suppression and extra excitation during walking, the activity of auditory neurons and receptors was recorded in the fixed animal during passive movement of a foreleg, with the arrangement shown in Fig. 7. The effects on interneurons are illustrated for ON1 in Figs. 8 and 9. At certain times during the passive movement, the interneurons were excited, and when acoustic stimuli were presented at the same time, this excitation was superimposed on the response. At other times during leg movement, the tonic response of the interneuron to a steady tone was suppressed. The contralateral ON1 – that is, the ON1 on the side of the leg that was not moved – also exhibited extra excitation at about the same times, but always to a lesser degree than with ipsilateral leg movement. No suppression of the response to steady tones was observed in the contralateral ON1.

Both the excitatory and the suppressive phenomena associated with passive leg movement re-

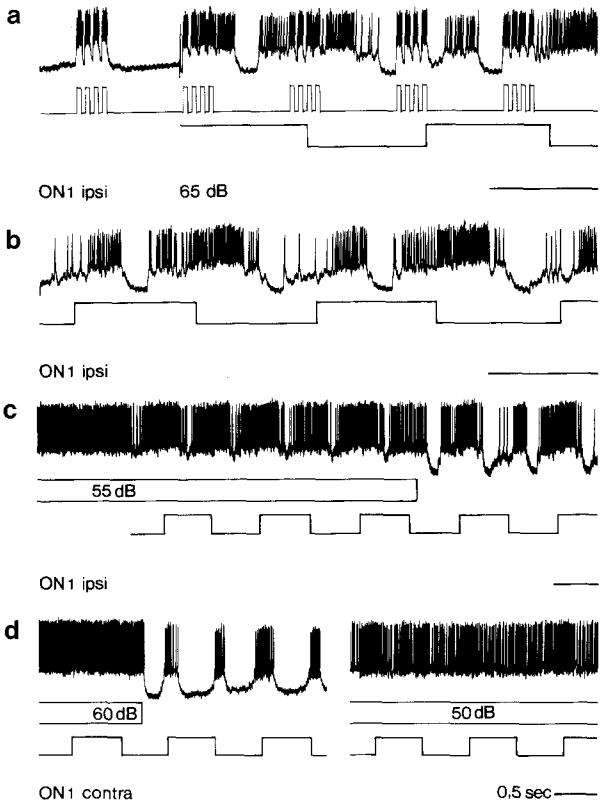

Fig. 8a–d. Recordings from the ON1 ipsi- and contralateral to the leg moved passively during sound stimulation. **a** Responses of the ipsilateral ON1 (top trace) to calling song (middle trace) and passive leg movement (lower trace, alternating direction during movement; defined in Fig. 9); **b** responses to leg movement without sound stimulus; **c** responses to a steady tone (5 kHz) with and without passive leg movement, showing suppression of the response to the tone in certain phases of the movement; **d** response of the contralateral ON1 to a steady tone and passive leg movement

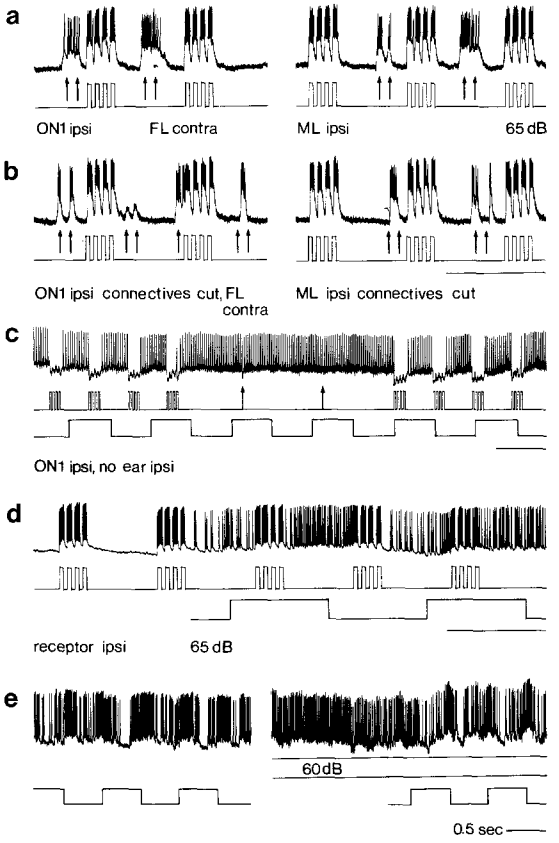

Fig. 9. a Responses of an ON1 to calling song and touching (arrows) the ipsi- or contralateral foreleg (*FL*) and the ipsilateral middle leg (*ML*). **b** Like **a**, after transection of the connectives between pro- and mesothoracic ganglion. **c** Response of the left ON1 to calling song after transection of the left auditory nerve, with passive movement of the left leg. The cell is slightly depolarized and has a tonic discharge; because of the inhibitory influence of the intact contralateral ear, the sound stimulus elicits only inhibition, and the massive excitatory and suppressive effects of passive leg movement are no longer observable except for a brief but reproducible interruption of the tonic discharge at certain times (arrows). **d** Responses of an auditory receptor cell to calling song during passive leg movement. **e** Responses of the receptor cell to a steady tone during leg movement. Passive leg movement exerts excitatory and suppressive influences on the receptor cell as well as on interneurons

mained unchanged when the tarsal segments and/or the distal tibial bristles were removed. Touching the ipsi- or contralateral foreleg produced excitation of ON1, as did touching any of the other legs, the thorax or the abdomen. This effect persisted after transection of the connectives between the pro- and mesothoracic ganglia (Fig. 9). After one posterior tympanum has been immobilized with wax, or after transection of the auditory nerve, the ipsilateral ON1 was inhibited by sound stimuli (Fig. 9c), an effect mediated by the contralateral ON1, the excitatory input of which was still intact. When the leg of an animal with waxed tympanum or transected auditory nerve was moved, the ON1 was no longer excited by the movement. It follows that the excitatory influence of passive leg movement on auditory neurons – at least under the conditions chosen here – derives from the oscillation of the tympanum and hence from the excitation of auditory receptors.

In animals with one ear blocked, there was no sign of suppression of neuronal activity at times at which passive movement suppresses auditory responses in animals with intact ears. Nevertheless, there was a brief but consistent interruption of the tonic discharge of the slightly depolarized neuron (Fig. 9c). The interruption occurred at a time when the neurons of animals with intact ears were excited by the leg movement. This suppression is possibly mediated by the contralateral ON1: Vibration caused by the movement of the ipsilateral leg had propagated into the contralateral leg, excited the ear, and thereby the contralateral ON1. The contralateral ON1 inhibits its partner cell. This in-

hibition becomes visible because the ipsilateral auditory nerve was cut.

The effects of passive leg movement on an auditory receptor cell are shown in Fig. 9d, e. There were distinct periods of excitation, correlated with the passive leg movement and occurring at about the same times as in the interneurons. This excitation was superimposed on the responses to calling song or steady tones. Surprisingly, even in the receptors the tonic discharge was suppressed at certain times during passive leg movement – again, at the same times as in the interneurons. Therefore suppression of the responses of auditory interneurons during passive leg movement could result – at least partly – from changes in the properties of the ear.

Discussion

The experiments described here have demonstrated that walking does exert a considerable influence on the cricket auditory system. The basic excitatory effect appears to result from vibrations produced when the leg is placed on the ground, which spread through the body and displace the tympanum. The evidence is twofold: this excitation is present at the most peripheral level, in the auditory receptors, and it disappears when the tympanum is immobilized or the foreleg does not touch the ground. Vibration is known to propagate considerable distances through the cuticle of arthropods (Barth, pers. comm.). Auditory interneurons of the cricket can be excited by touching any of the legs, even if the connective between the pro- and mesothoracic ganglion is cut. However, because we have no information about the vibrations that occur in the legs when the animal is walking in its natural surroundings, we cannot say whether this kind of interference with auditory signals also appears when the cricket walks in its habitat.

The excitation of auditory units by passive leg movement is probably also due to vibration in the leg. The uneven force of the metal ring on the leg changed sharply shortly after the direction of leg movement was reversed, and at this time the excitation in receptors and interneurons was most pronounced. The cells were also excited, at the same times, when the contralateral leg was moved. Under these conditions suppression was not observed. Blocking of the ipsilateral ear abolished the excitation associated with ipsilateral leg movement.

Movements – respiratory and stridulatory movements as well as passive movement of the hindlegs – have also been shown to excite auditory receptors in acridid grasshoppers (Hedwig et al. 1987). It appears that due to their mechanical coupling with the cuticle, the tympana of orthopterans are in general excited by the animal's own movements. But it is not clear whether this activation of the auditory system is an inevitable component of the 'noise' or serves as an additional source of proprioceptive information.

In principle, mechanoreceptors other than the auditory organ could also influence the response of auditory neurons during walking. Receptors in the subgenual organ, located in the tibia, are very sensitive to vibration (Dambach and Huber 1974). There are vibration-sensitive central neurons that integrate the vibration information from all six legs (Kühne et al. 1985), and vibrational stimuli have been shown to have an excitatory as well as inhibitory influence on auditory neurons in crickets, bushcrickets and grasshoppers (Kalmring et al. 1985; Kühne et al. 1985; Wiese 1981). But no direct evidence that vibration receptors excite or inhibit auditory neurons during walking has yet been produced.

The suppression of the response of auditory neurons to sound in certain phases of the leg movement might be produced by the inhibitory influences of other central neurons. The two mirror-image ON1 neurons are reciprocally inhibitory (Selverston et al. 1985). During walking this inhibition is exerted when the contralateral leg is placed on the ground, and therefore the auditory response is suppressed at that time.

But an additional central component may be involved as well, because suppression also occurs during 'four-legged' walking. The suppression in these animals is unlikely to be the result of the reciprocal inhibition of the omega neurons because there is no walking-induced excitation in the ON1 and hence no contralateral inhibition. On the other hand, we cannot rule out definitely that changes in the sensitivity of the auditory organ can occur during walking even in animals with fixed forelegs because recordings from receptor cells are lacking for this situation. The responses of auditory receptor cells are also suppressed in a phase-coupled manner by passive leg movement. There is some doubt as to the possibility of efferent control of the auditory organ in crickets, because no synaptic structures have yet been found in the ear (Michel 1974). However, efferent catecholamine-containing neurons that run close to the auditory organ have been described (Popov and Svetlogorskaja 1979). Both passive and active leg movements could alter the pressure relationships at the tympanum, in the

acoustic trachea, or at accessory structures of the auditory organ, and thereby influence the transduction mechanism.

Modulation of sensory information during an animal's own movement has been studied in many systems and both peripheral and central components seem to be involved (Pollack and Henson 1973; Müller-Preuss and Ploog 1981; Wolf and von Helversen 1986; Hedwig 1986; Daley and Delcomyn 1980). It appears, then, that central as well as peripheral modulation of sensory information during movement occurs in many animal groups and very diverse sensory systems.

Modulation of the auditory information while a cricket is walking could have some significance with regard to its ability to track a sound source. Weber et al. (1981) found that only 2 of 10 animals could track calling song if it was available only during walking. In open loop experiments it is shown that crickets can follow a change of speaker direction without a walking stop (Schildberger and Hörner 1988). Whether unrestrained or fixed, some crickets do not need to stop in order to localize the sound source of a calling song. At high intensities neuronal responses to the calling song are always visible during walking. At lower sound intensities, however, perception of the calling song is considerably disturbed during walking.

It may be that the cricket compensates for interference in the auditory pathway by suitably adjusting its behavior in two different ways. First, localization of sound sources can be eased by frequent walking stops which typically occur during phonotactic walking (Weber et al. 1981; Schmitz et al. 1982). Second, while walking continuously the animal could take advantage of the time window described here, if it walks at a sufficiently low speed.

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