J Comp Physiol (1983) 153:523–532

Journal
of Comparative
Physiology · A

Peripheral auditory directionality in the cricket (*Gryllus campestris* L., *Teleogryllus oceanicus* Le Guillou)

Paul Boyd* and Brian Lewis**
Department of Biological Sciences, City of London Polytechnic, Calcutta House, Old Castle Street, London E1 7NT, England

Accepted August 11, 1983

Summary. 1. The directionality of the auditory organ in the crickets *Gryllus campestris* and *Teleogryllus oceanicus* was investigated by recording auditory responses in the prothoracic leg nerve using a whole-nerve recording technique.

2. In both species the occurrence of substantial left-right directionality was maximal at frequencies around the carrier frequency of the respective calling songs (Figs. 3, 6).

3. Blockage experiments indicated that the input of sound into the auditory system via the acoustic spiracles was more important than the input via the contralateral tympanum (Figs. 4, 8); blockage of both spiracles eliminated almost all directionality, whereas blockage of the contralateral tympanum had very little effect.

4. Unilateral spiracular blockage demonstrated that input from both spiracles is necessary for a normal directionality pattern. Blockage of the contralateral spiracle reduced the maximum left-right difference from 28 dB, in the intact state, to 8 dB. Ipsilateral spiracular blockage produced a supercardioid directionality pattern (Fig. 5).

5. Investigations into the transmission of sound to the rear surface of the posterior tympanum via the spiracles and the contralateral tympanum confirmed, for both species, that the spiracles provide greater input into the auditory system than the contralateral tympanum. The ipsilateral spiracle provides a slightly greater input than the contralateral spiracle (Fig. 9).

Introduction

The phonotaxis of a female cricket towards a conspecific singing male has been described by many workers (Murphey and Zaretsky 1972; Bailey and Thomson 1977; Wendler et al. 1980). This behaviour firstly necessitates recognition of a sound as that of a conspecific male, and then localization of the sound source, in order to decide in which direction to walk. This localization has been shown behaviourly to be primarily a function of the frequency component of the song (Hill 1974; Rheinlaender and Blatgen 1982; Thorson et al. 1982). In contrast to most other Ensifera, the gryllids produce songs that are essentially narrow-banded and of relatively low frequency (Nocke 1972; Hill 1974; Popov and Shuvalov 1974). Little sound diffraction can be produced around the body of the insects at these frequencies, and a special mechanism for localization of such sounds is therefore needed.

The auditory organs of crickets are located in the tibiae of the forelegs. The sensory cells of each organ are stimulated via a tympanum which is formed from a thin region of the leg cuticle in contact with the wall of the modified leg trachea. The proximal end of this trachea opens at an 'acoustic spiracle' on the prothorax. Near the spiracle, a branch of the trachea extends centrally, abutting at the midline with the branch from the opposite side (Michel 1974; Young and Ball 1974; Zhantiev et al. 1975). The two auditory organs have been shown to be acoustically coupled (Zhantiev et al. 1975; Hill and Boyan 1976, 1977), thus there are four possible routes for access of sound to each tympanum.

The *localization* of a sound by these insects is carried out by the central nervous system on the

---

* Present address: Department of Neurophysiology, School of Biochemistry and Physiology, University of Southampton, Southampton S09 3TU, England

** To whom offprint requests should be sent basis of *directional cues* provided by the auditory organs. In order to provide directional cues the responses of the auditory organs must vary with the angle of incidence of the sound. The extent to which this can be achieved defines the *directionality* of the auditory organs. The aim of this study was to establish the extent of this directionality in the crickets *Gryllus campestris* and *Teleogryllus oceanicus*, and to determine its basis.

The experiments of Hill and Boyan (1977) showed the occurrence of directionality to be restricted to frequencies around the calling song carrier frequency in *Teleogryllus commodus*, and postulated a mechanism based on transmission of sound across the body from one auditory organ to the other. However, some of the details of this model have been questioned by the results of certain other workers (e.g. Larsen and Michelsen 1978; Kleindienst et al. 1981). The present study attempts to resolve some of these problems.

Materials and methods

Investigations into the directionality of the auditory organ were carried out on 56 specimens of *G. campestris*, together with a small number of experiments (7), for comparative purposes, on *T. oceanicus*. Adults of both sexes were used, at least one week after their final moult. Both species were maintained as cultures within the laboratory.

Following removal of the wings and antennae the insects were waxed, in the natural standing position, to a vertical stand made of 0.8 mm wire. This held the insect at a height of 25 cm above a small baseplate and at the centre of an anechoic chamber of internal dimensions 2.5 x 2.5 x 2.2 m. A calibrated loudspeaker (Kef HD17/HR37 for frequencies up to 10 kHz; Audax TW8B for frequencies above 10 kHz) mounted on a metal boom of rotation radius 1.0 m could be rotated in the horizontal plane from outside the chamber. The sound field at the centre of the chamber was uniform to within ±2 dB up to 40 kHz. The ambient temperature was 24±2 °C.

Recordings of auditory responses in the prothoracic leg nerve were made using the method employed by Stephen and Bailey (1982) working on bushcrickets. Whole-nerve recordings of auditory responses were obtained from the sensory branch of the prothoracic leg nerve, just above the genual joint, using an electrode consisting of a short length of 0.002 in. uncoated silver wire (Clark Electromedical Instruments). Although the sensory branch of the leg nerve is separate from the motor branch in the femur (Eibl and Huber 1979) it was found necessary to section the main leg nerve in the coxa to decrease background nervous activity. A 0.2 mm uncoated silver wire, inserted into the abdomen, served as an indifferent electrode.

Evoked responses to sound stimuli of 20 ms duration and 5 ms rise/fall time were averaged over 128 presentations (Neurolog NL750) and plotted on a chart recorder (Mingograf 800). The acoustic stimuli were produced using a tone-burst generator built in the laboratory from a design by Taylor (1978), and were presented at a rate of 9/s, which was found to cause negligible adaptation.

The majority of the experiments were concerned with investigating directionality around the carrier frequency of the calling song. At each frequency tested an intensity-response curve was first constructed by measuring the maximum peak-to-peak amplitudes of the chart-recorder traces of the responses obtained, over a range of intensities, with the loudspeaker ipsilateral to the recorded ear (Fig. 1). Sound pressures are expressed as dB relative to 2×10^{-5} Pa. Directionality was then determined by recording the responses to stimuli of 20–30 dB above ipsilateral threshold when these were presented at several angles around the insect in the horizontal plane. The amplitudes of these responses were converted to effective dB using the intensity-response curve for the relevant frequency. Higher sound pressures were used when the loudspeaker was contralateral to the recorded ear in order to remain in the more linear region of the intensity-response curve.

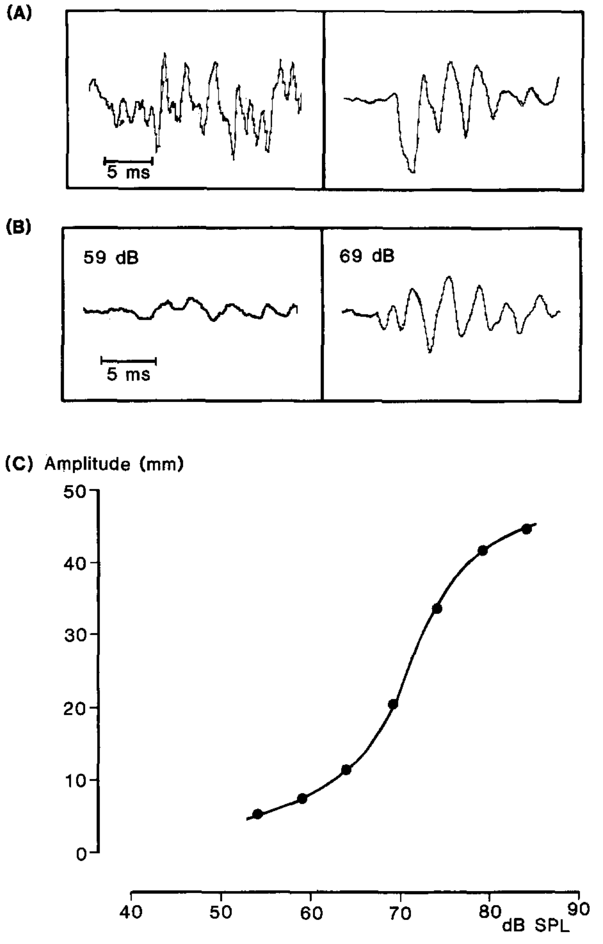

Fig. 1 A–C. Construction of an intensity-response curve for *G. campestris* at 4.7 kHz. **A** Original waveform obtained to 4.7 kHz at 75 dB after one presentation (left) and the averaged response obtained after 128 presentations (right), plotted on the chart recorder. **B** Examples of neural responses averaged over 128 presentations at 59 and 69 dB, from a different specimen to that in (**A**). **C** A representative intensity-response curve constructed with the loudspeaker ipsilateral to the recorded ear. Amplitudes given were obtained from the chart-recorder traces

As well as determining the directionality of the intact peripheral auditory system an attempt was made to determine the contributions of the various sites of sound entry into the auditory system. Most experiments involved blocking tympana or spiracles with wax and measuring the resultant changes in directionality or overall sensitivity. Contralateral as well as ipsilateral inputs were investigated. Anatomical structures are hereafter termed as ipsilateral or contralateral to the recorded ear.

Results

Threshold values

The loudspeakers used allowed the testing of auditory thresholds at frequencies up to 40 kHz. Thresholds were tested in 3 specimens of *G. campestris* and an example is given in Fig. 2. The technique employed is not ideal for threshold determinations as the response near threshold becomes lost in background noise. Thresholds were taken as the lowest sound pressure for which the averaged response was visible above background activity after 128 presentations, but the real thresholds of the auditory organ may be a few dB below the values shown. Nevertheless, relative sensitivities are clear; although the auditory organ can be seen to be responsive to sound frequencies of up to 40 kHz a major peak of sensitivity is evident near 5 kHz, with a lesser peak around 15 kHz. These correspond to the carrier frequencies of the calling and courtship songs respectively, as shown by Nocke (1972).

Directional responses in G. campestris

Directionality of the intact system. Figure 3A shows a typical series of plots from a single preparation showing directional variation in the responses at several frequencies around the calling song carrier frequency. Responses are shown as dB relative to 0° (anterior). This is because it is assumed that the two auditory organs have mirror-image response patterns that overlap anteriorly (and posteriorly). In each case the 90° position is ipsilateral. From 4.5 kHz directionality increases with frequency, to a maximum at 4.8 kHz, where the response pattern is 'cardioid', with a 'null' at 260°. Above this 'best frequency' the directionality declines, in terms of maximum left-right (L-R) difference, and the pattern becomes almost omnidirectional at 5.2 kHz. Maximum L-R difference may be used as a rough quantitative measure of directionality and is used here as the difference, in dB, between the maximum response on the ipsilateral side and the minimum response on the contralateral side (not necessarily at exactly 90° and 270°). By using a monitor loudspeaker to listen to the response it was possible to locate the null, or position of minimum response, precisely in both spatial position and frequency. Plots at the best frequency were constructed for several specimens.

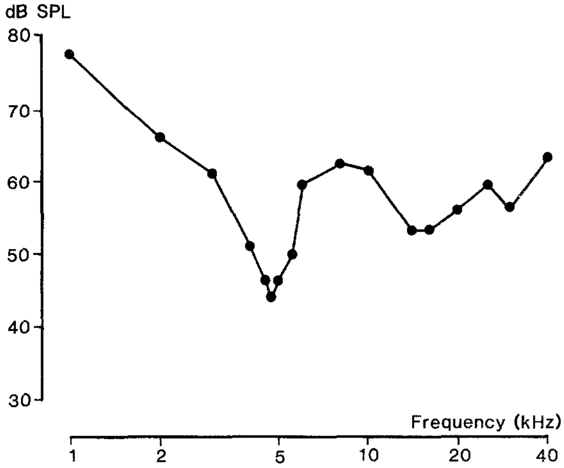

Fig. 2. Thresholds of the auditory organ of *G. campestris* to ipsilaterally presented sound (re. 2×10^{-5} Pa)

The mean value of the best frequency was 4.92 kHz (range 4.4–5.3 kHz, $n=23$), the angle of the null was 268.7° (range 240°–300°, $n=23$) and the maximum L-R difference was 27.9 dB (range 18–35 dB, $n=21$). No correlation was found between best frequency and the size of the insects.

Although it was possible to accurately locate the position of minimum response there was some variation in its depth between specimens, as is illustrated by the range of the maximum L-R difference. In a small number of specimens (5) a 'supercardioid' pattern was observed at the best frequency (Fig. 3B). Whenever this occurred all other features of the directionality, such as its development around the calling song carrier frequency, were identical to those observed for specimens showing cardioid directionality.

The effects of contralateral tympanum blockage. The effects, on directionality, of preventing sound entry into the auditory system via the contralateral posterior tympanum was tested by blocking it with wax in 12 specimens, an example being given in Fig. 4A. The anterior tympanum was assumed to be non-functional (Nocke 1972; Larsen and Michelsen 1978). Blockage of sound entry via the contralateral tympanum in this way did not affect the magnitude or shape of the directionality. In a few cases the best frequency was shifted to a slightly lower value during tympanal blockage. This was precisely measured in 5 specimens; for these specimens the mean best frequency in the intact state was 4.65 kHz, and the best frequency with the contralateral tympanum blocked was 4.49 kHz, but this change was not statistically significant ($p=0.23$, paired t-test).

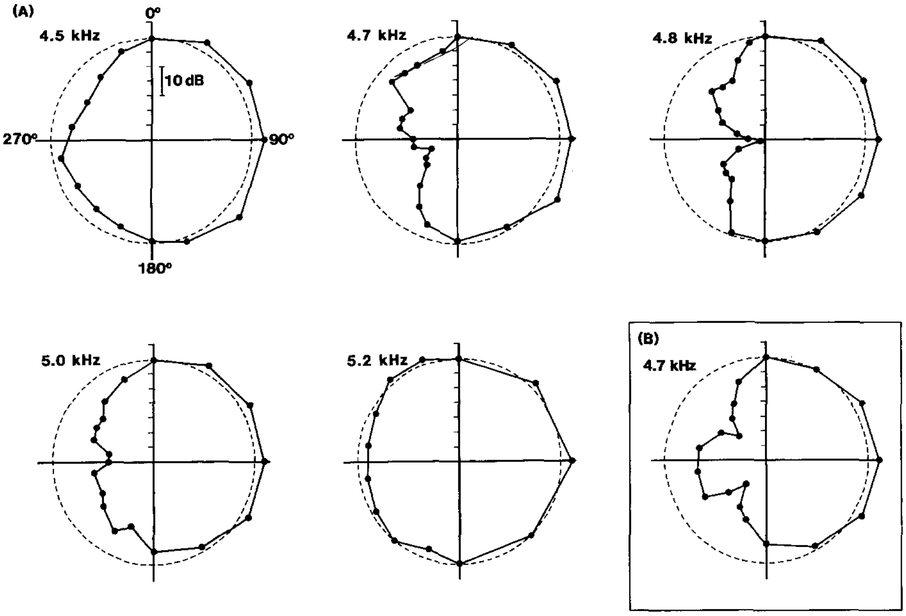

Fig. 3. A Development of peripheral directionality of the auditory organ of *G. campestris* at frequencies around the calling song carrier frequency. **B** Example of a supercardioid pattern at the best frequency (4.7 kHz). Data in series (**A**) from a different specimen to that in series (**B**)

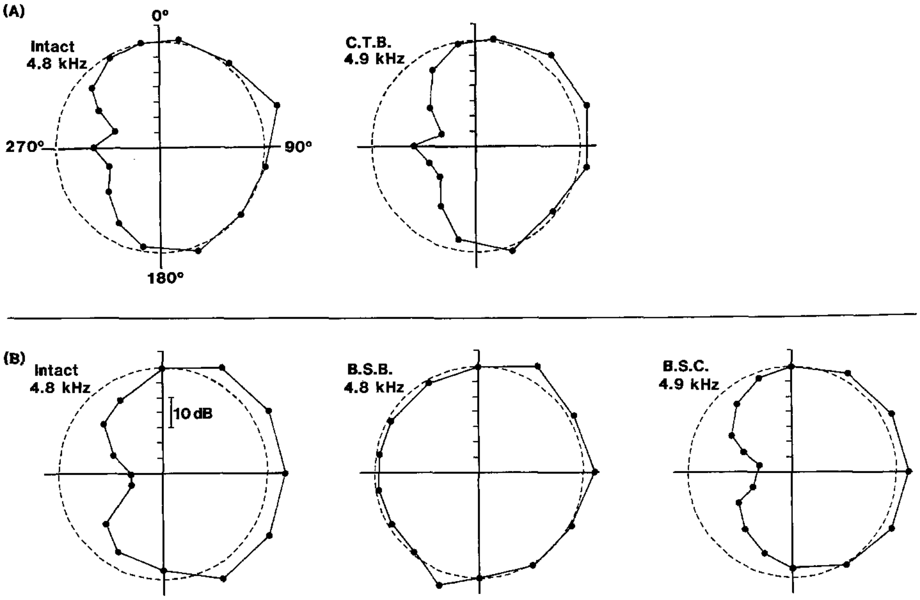

Fig. 4A and B. Effect of blockage of the contralateral tympanum and of the spiracles on directionality patterns in *G. campestris*. **A** Plots at the best frequency in the intact state and with the contralateral tympanum blocked (CTB). **B** Plots at the best frequency in the intact state, with both spiracles blocked (BSB), and with both spiracles cleared (BSC). After clearance in (**A**) and (**B**) the best frequency had shifted by 100 Hz

The effects of bilateral spiracular blockage. Blockage of both acoustic spiracles always eliminated almost all directionality. This test was performed on 10 specimens, and a typical result is shown in Fig. 4B. At no frequency could any greater L-R difference be found during spiracular blockage, the average L-R difference being 5 dB ($n = 7$). On clearing the spiracles of wax the response pattern returned to its original form.

The effects of unilateral spiracular blockage. It was considered a possibility that during experiments involving unilateral spiracular blockage the insect may respond to wax blockage of one spiracle by closing its other spiracle. Therefore, these experiments were conducted with the relevant spiracle waxed slightly open to prevent this possibility. Blockage of the contralateral spiracle alone, carried out in 9 specimens, typically produced a response pattern as in Fig. 5A, where most of the original L-R difference has been lost. It was not possible to improve the directionality by changing the frequency of the stimulus. The mean maximum L-R difference under these conditions was 8.25 dB ($n = 9$). Clearance of the spiracle returned the pattern to its original form.

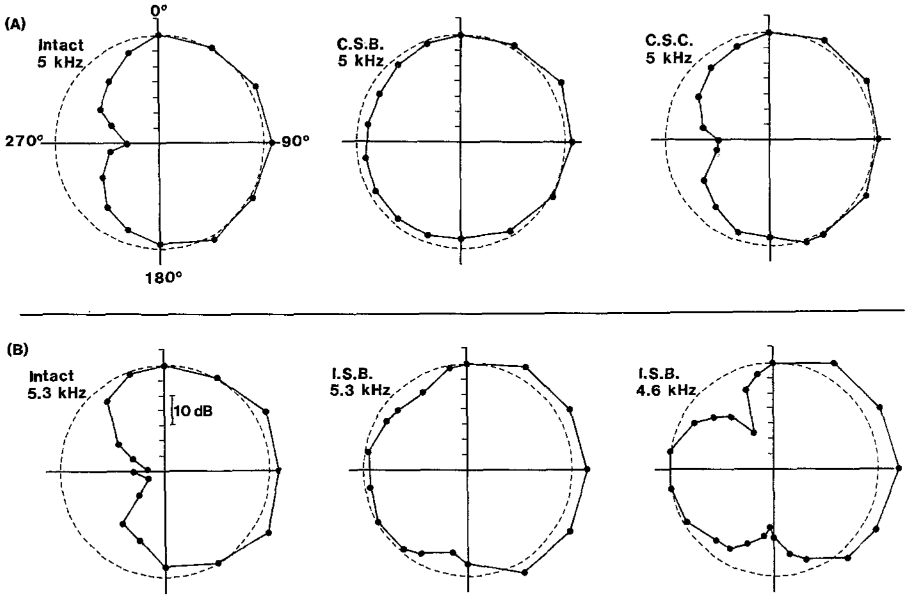

Fig. 5A and B. Effect of unilateral spiracular blockage on directionality patterns in *G. campestris*. **A** Plots at the best frequency in the intact state, with the contralateral spiracle blocked (CSB), and with the contralateral spiracle cleared (CSC). **B** Plots at the best frequency (originally 5.3 kHz) in the intact state, with the ipsilateral spiracle blocked (ISB, centre), and after also changing the sound stimulus frequency to 4.6 kHz (ISB, right). Data in series (**A**) from a different specimen to that in series (**B**)

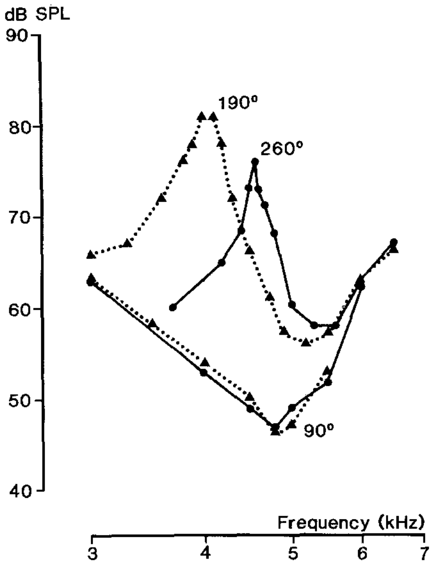

Fig. 6. Thresholds of the auditory response measured at 90° (ipsilateral) and at the position of the null in the intact state (260°) ●——●, and after blockage of the ipsilateral spiracle (190°) ▲···▲

Following blockage of the ipsilateral spiracle most directionality was lost, but there was some suggestion of a supercardioid pattern (Fig. 5B). The contralateral response diminutions were 5–10 dB, relative to the 0° position, in most preparations. It was found that paired nulls occurred that were consistently tuned to a lower frequency than the cardioid null of the intact state. In Fig. 5B the normal cardioid pattern occurred at 5.3 kHz. During blockage of the ipsilateral spiracle the directionality was greatly reduced, but changing the frequency to 4.6 kHz produced a supercardioid response pattern with nulls at 195° and 330°. Each of these paired nulls were always tuned to approximately the same frequency, and this frequency was a mean of 650 Hz lower than the respective intact state best frequencies (this drop was highly significant: $p<0.001$, $n=6$). The supercardioid nulls had a mean separation of 119°, centred about the 262° position ($n=12$). For these specimens the mean position of the intact state null was 271°, but this was not statistically different from the position at the centre of the supercardioid nulls (262°) when the ipsilateral spiracle was blocked ($p=0.245$). There was no evidence that changing the stimulus frequency altered the positions of the nulls – only their sharpness was affected. When this test was performed on a specimen that showed a supercardioid pattern in the intact state, ipsilateral spiracular blockage produced a pattern with nulls that were more widely spaced and tuned to a lower frequency than in the intact state.

Thresholds to frequencies around the best frequency of the null were determined in the intact state for 3 specimens with the loudspeaker (a) at the 90° ipsilateral position and (b) at the position of the null. A typical result is given in Fig. 6. The difference between the thresholds at the ispilateral and null positions effectively shows the tuning of the intact state directionality. This was repeated with the ipsilateral spiracle blocked; blocking the spiracle did not affect the thresholds at the 90° position but the null can be seen to be tuned to a lower frequency. Thresholds shown are for only one of the nulls occurring with the spiracle blocked, as both showed the same thresholds.

The tuning of the nulls. The change in the suprathreshold response with frequency was tested at the position of the null(s) in the intact state and during various test situations in 7 specimens. In each case the null was first located spatially, and then the responses to various constant intensity frequencies around the null frequency were measured. In the example shown (Fig. 7) the tuning of the null is shown in the intact state, after blockage and after clearance of the contralateral tympanum, and after blockage and after clearance of the ipsilateral spiracle. Responses were converted to dB from an intensity-response curve constructed at the respective null frequency. The null in the intact (cardioid) state was tuned to 4.85 kHz. After contralateral tympanum blockage there was a slight decrease in the null frequency to 4.8 kHz, which increased to 4.9 kHz after clearance.

Blockage of the ipsilateral spiracle produced a supercardioid directionality pattern, with nulls at 185° and 315°. These nulls can be seen to be tuned to 4.3 kHz and 4.2 kHz respectively. Clearance of the spiracle returned the directionality to cardioid form with a null tuned to 4.9 kHz. It should be noted that as the points for each tuning curve were converted to effective dB from an intensity-response curve produced at the null frequency there will be small errors in the points recorded off the null frequency as the intensity-response curves are not identical at all frequencies.

Directional responses in T. oceanicus

Most of the experiments described for *G. campestris* were repeated, for comparative purposes, on *T. oceanicus*. The results were essentially identical and a summary is provided by Fig. 8. It can be seen that blockage of the contralateral tympanum has no appreciable effect, whereas bilateral spiracular blockage abolishes most of the directionality. The mean value of the best frequency in the intact state was 4.74 kHz ($n = 4$). The directionality appears to be produced, as in *G. campestris*, by pressure-gradient interaction at the tympanum, the back-pressure being provided mainly by sound entering via the spiracles. The results of unilateral spiracular blockage were the same as described for *G. campestris*.

Transmission through the interaural pathway

Transmission of sound to the rear surface of the posterior tympanum was investigated by waxing

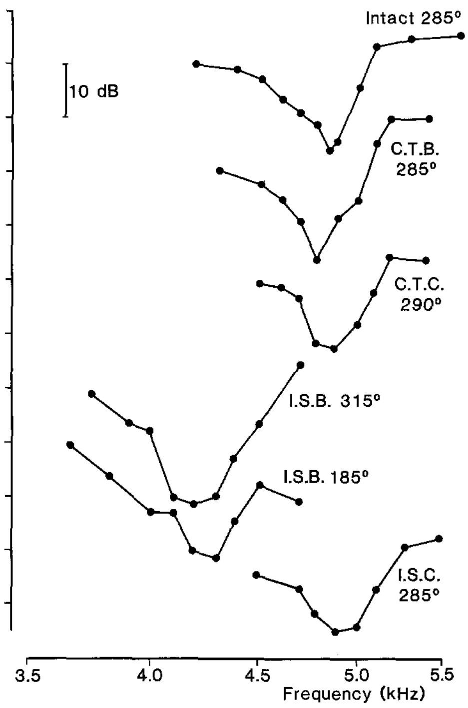

Fig. 7. Variation in null tuning curves at the positions given, under several conditions, for a representative specimen of *G. campestris*. Intact – intact state; *CTB* – with the contralateral tympanum blocked; *CTC* – with the contralateral tympanum cleared; *ISB* – with the ipsilateral spiracle blocked; *ISC* – with the ipsilateral spiracle cleared. Responses for each plot were converted to dB from the intensity-response curve of the respective null frequency. Ordinate is non-continuous and curves are vertically displaced for clarity

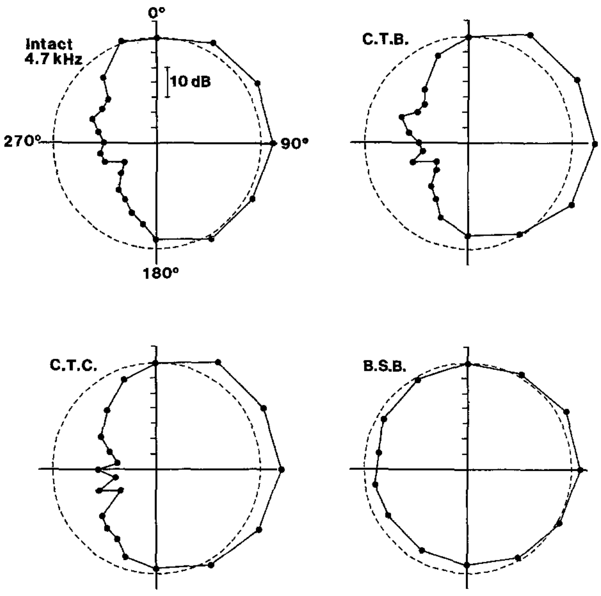

Fig. 8. Directionality patterns in *T. oceanicus* at 4.7 kHz. Plots are given for the best frequency in the intact state, with the contralateral tympanum blocked (*CTB*), with the contralateral tympanum cleared (*CTC*), and with both spiracles blocked (*BSB*). All data from one specimen

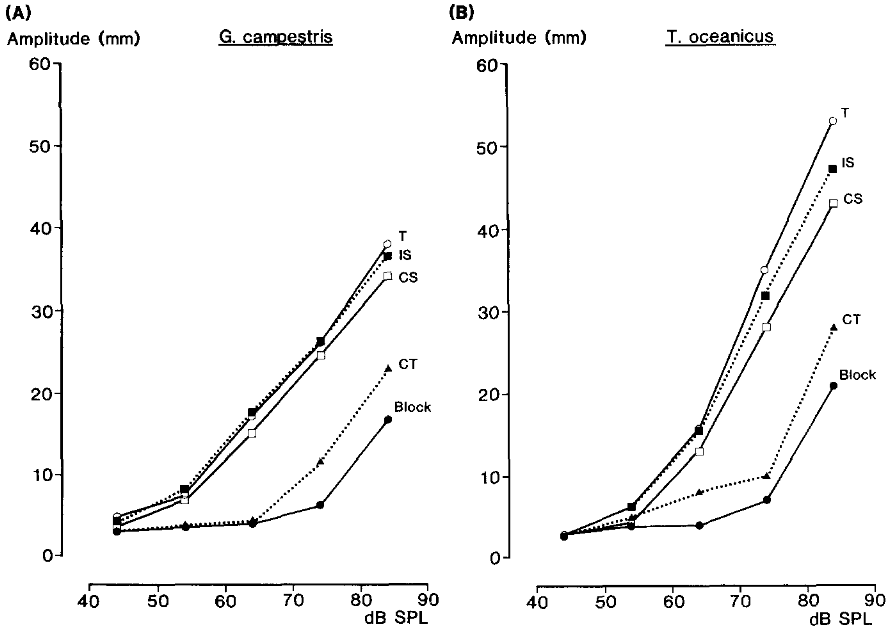

Fig. 9A and B. Intensity-response curves for ipsilaterally presented sound with a plastic tube around the ipsilateral tibia for 6 specimens of *G. campestris* (**A**) and 1 specimen of *T. oceanicus* (**B**). *T*, curve constructed with all other sound input sites open; *IS*, with the ipsilateral spiracle alone open; *CS*, with the contralateral spiracle alone open; *CT*, with the contralateral tympanum alone open; *Block*, with all input sites blocked. Stimulus frequency = 5 kHz

a sleeve of plastic tubing around the ipsilateral tibia, to prevent sound access to the front surface, and comparing the sensitivity of the auditory organ to sound entering the auditory system via the two acoustic spiracles or the contralateral tympanum (hence incident on the rear surface of the tympanum). As the experimental method was not ideal for measuring thresholds, intensity-response curves were constructed under several conditions to compare sensitivities. Figure 9A shows mean values for 6 specimens of *G. campestris* for ipsilaterally presented sound. T is the intensity-response curve produced with all three inputs open (the ipsilateral and contralateral spiracles and the contralateral tympanum). IS, CS, and CT are the curves produced with the respective input sites open individually, the other two inputs being blocked with wax in each case. The 'block' curve was produced with all inputs blocked. Figure 9B gives the results of a single experiment on *T. oceanicus*. It is evident, for both species, that with either spiracle open substantial back-pressure is produced which is almost as great as that produced with all three inputs open. The input from the ipsilateral spiracle produced a slightly larger response than that from the contralateral spiracle. The contribution of the contralateral tympanum was considerably smaller, however, being only slightly greater than that produced in the totally blocked condition. The response in the latter case was probably due to resonance of the leg by the wire frame as it was very consistent and did not appear above threshold levels until about 70 dB SPL.

When sound was presented contralaterally the sensitivity to sound entering via the single inputs changed in accordance with expectations based on sound diffraction, i.e. the sensitivity to the contralateral inputs increased by 1–2 dB while the sensitivity to the ipsilateral input decreased by a similar amount. The ipsilateral spiracle still produced a slightly larger response than the contralateral spiracle. However, the sensitivity to sound entering via all three inputs together (T) was less by about 10 dB, in *G. campestris*, indicating some phase interaction between the three inputs. The curve for the totally blocked condition was the same as for ipsilaterally presented sound.

Discussion

The experimental technique employed in this study has two distinct advantages over other methods of physiologically determining peripheral directionality. Firstly, investigations are carried out on an almost intact insect whose legs were waxed in the natural standing position; secondly, the responses remain reasonably stable over a long period of time, thereby enabling many successive tests to be made on one specimen. The main disadvantage is that the responses cannot be quantified directly, but must be quantified by converting the amplitudes to dB from an intensity-response curve. Thus directional plots show the directionality available to the receptor (i.e. the peripheral directionality), as may be obtained by measuring the thresholds of any auditory neurone at different angles of sound incidence.

The information that is utilized by the insect from the available peripheral directionality will depend upon the absolute thresholds and dynamic ranges of single units, and the degree of intensity range fractionation in the auditory pathways. From the intensity-response curves produced in this study (e.g. Fig. 1) it is clear that the receptors may code the intensity of sound at the calling song carrier frequency over a range of about 60 dB. Single-unit studies have shown primary and central neurones with dynamic ranges of 25–35 dB that show range fractionation sufficient to code intensity over at least 50 dB (Boyan 1979; Esch et al. 1980; Hutchings and Lewis 1981). There is also evidence that the peripheral directionality may be coded in terms of response latency (Nocke 1972; Mörchen et al. 1978).

The development of cardioid directionality around the carrier frequency of the calling song (Fig. 3) is similar to that reported by Hill and Boyan (1977) for *Teleogryllus commodus*. In *G. campestris* an appreciable L-R difference was usually evident between about 4 kHz and 6 kHz, but differences of more than 10 dB were restricted to frequencies within a band of some 300 Hz either side of the best frequency.

The directionality patterns of most specimens were cardioid, but there was variation in some of the characteristics of these patterns at their respective best frequencies. The position of the null, while occurring at about 270° on average, varied from about 240° to 300°. Since the alignment of the preparations, including their leg positions, varied by less than 5° this variability could correspond to the left-right asymmetry measured physiologically by Boyan (1979) and behaviourally by Hoy and Paul (1973). However, bilateral recordings are necessary to test this possibility. The frequency that produced the greatest L-R difference ('best frequency') was at a mean of 4.92 kHz in *G. campestris*, with a range from 4.4 to 5.3 kHz. Kleindienst et al. (1981) showed transmission of sound to the rear surface of the posterior tympanum to be best at a mean of 5 kHz, but with a range extending from 3.15 to 5.6 kHz. This might explain the range in best frequency found in the present study.

In a few specimens, supercardioid patterns were found in the intact state. In order to produce a perfect null by pressure-gradient interaction the phase and pressure of the sound incident on the front and rear surfaces of the tympanum must be equal (Hill and Boyan 1977; Larsen and Michelsen 1978). If the phase angles of the sounds are equal, but the sound pressures, are not, an imperfect null will be produced, although the directionality pattern could still be cardioid. Furthermore, in the ideal situation, the sound components acting on the two surfaces of the tympanum should change from being out of phase to being in phase (0° relative phase) when the sound source is moved from the ipsilateral to the contralateral position. If the relative phase at the contralateral position does not reach 0° a cardioid pattern with an imperfect null will result; if the relative phase reaches 0° before the contralateral position a supercardioid pattern with perfect nulls will result (assuming that the sound pressures are equal).

Thus the variation in the cardioid patterns observed, and the occurrence of supercardioid patterns, may be explained on the basis of imperfect matching of the pressure and/or phase of the sound components interacting at the tympanic membrane. One possible reason for this mismatch could be that since the position of the null was rarely exactly on the interaural axis it may also have been rarely located exactly on the horizontal plane. No investigations into the effects of elevation were made.

The directionality patterns constructed at the best frequencies represent the maximum degree of directionality possible in the horizontal plane. It is clear from Figs. 3, 6 that this may only be achieved at one frequency; even sound 100 Hz away from the best frequency will produce a maximum L-R difference that is reduced by several dB. The main energy peak in the calling song of *G. campestris* extends over about 500 Hz, between about 4.5 and 5.0 kHz, so that directional variation in the responses to the species song will probably be less than to the best pure-tone frequency.

The results of investigations involving manipulations of the auditory system by blockages need to be interpreted with caution as blockage of one input may change the acoustic properties of the system for sound entering via other input sites (Larsen and Michelsen 1978). In the present study this is particularly true for blockage of the ipsilateral spiracle; its blockage may change the impedance of the acoustic spiracle. It is of interest, however, to consider such results in the context of behavioural experiments conducted under the same conditions.

With these points in mind, it is clear that little directionality is achieved when both the spiracles are occluded, whereas blockage of the contralateral tympanum had very little effect (Figs. 4, 8). These findings are contrary to those of Hill and Boyan (1977) who found, in *T. commodus*, that either the spiracular inputs or the contralateral tympanum input alone provided a back-pressure at the tympanum sufficient to provide considerable directionality, although all the inputs were required for a normal response pattern. It is unlikely that the difference in these findings is due to species differences. *T. commodus* is very similar, morphologically, to *T. oceanicus*, which produced very similar results to *G. campestris* in the present study. There have been no other reports of differences in auditory processing of these frequencies between these species.

The effects of unilateral spiracular blockage show that both inputs are necessary to produce a normal directionality pattern (Fig. 5). Sound access to the rear surface of the tympanum via the ipsilateral spiracle alone would not be expected to produce much directionality by pressure-gradient interaction at the tympanum because the difference in the path lengths of the sound components is never very long (although it is possible that additional phase changes could be produced by the morphology of the trachea). The mean value of 8.25 dB, for the maximum L-R difference with the contralateral spiracle blocked, is close to the figure of 9 dB calculated theoretically for this condition by Thorson et al. (1982).

Sound input via the contralateral spiracle alone (ignoring the contribution of the contralateral tympanum) produced a supercardioid directionality pattern that was strongest at a frequency lower than the intact state best frequency. It is possible that blockage of the ipsilateral spiracle changes the best frequency of transmission across the body, thereby changing the tuning of the directionality. In any case, the system does not seem to act in the same way as the 2-input pressure-gradient system described for various vertebrates (e.g. Coles et al. 1980; Feng and Shofner 1981) because the separation of the paired nulls of the supercardioid patterns did not change with frequency. The same is true of the supercardioid patterns observed in intact preparations. If one spiracle of a free-walking cricket is blocked, the ear ipsilateral to the blockage will have supercardioid directionality while the other will show almost omnidirectional responses (Fig. 5). Assuming that the insects use the point of maximum response difference between the two ears for localization, it might be expected that such an insect would show errant phonotaxis towards the unblocked side, as no nulls can occur on the blocked side. There may also be some front/rear error, as there will be two positions of maximum L-R differences. Wendler et al. (1980) showed behaviourly that *G. campestris* females with one blocked spiracle tracked a target along a path that was at an angle to the correct course, the error being always towards the intact side. They did not, however, report any front/rear confusion.

The comparison of the thresholds at the 90° position and at the null (Fig. 6) indicates the variation in L-R difference with frequency, and shows that the intact state null occurs at approximately the same frequency as that to which the auditory organ is most sensitive. Blockage of the ipsilateral spiracle produced supercardioid directionality with nulls tuned at a lower frequency than in the intact state (Fig. 7), but it is clear from Fig. 6 that such blockage does not affect the tuning of the auditory organ, as measured by ipsilateral thresholds. In the example shown the auditory organ was tuned to 4.9 kHz in both the intact state and when the ipsilateral spiracle was blocked.

The transmission experiments described were performed as a further test for any species differences between *G. campestris* and *T. oceanicus.* They confirm that the magnitude of the back-pressure provided by the spiracular inputs is considerably larger than that from the contralateral tympanum. While some of the results of Hill and Boyan (1977) do not agree with those of the present study, the results of their transmission experiments are mostly in agreement with those described here (see their Fig. 2). The findings of the present study also suggest that the ipsilateral spiracle allows more sound input than the contralateral spiracle (as postulated by Larsen and Michelsen 1978). However, this does not necessarily mean that the ipsilateral spiracular input is the more important in providing directionality, as phase changes are at least as important as pressure levels.

The total back-pressure, i.e. the sound reaching the rear surface of the tympanum via all three possible sites together, varied considerably with the direction of the sound source. This indicates that the magnitude of the back-pressure, as well as its phase, changes with sound direction, which is another observation demonstrating that pressure-gradient function in these insects is more complex than the 2-input pressure-gradient system of other animal groups. Clearly, any model based on the dimensions of the auditory system of these crickets (e.g. Hill and Boyan 1977) must be at best incomplete, as no correlation between insect size and calling song carrier frequency has been demonstrated. Factors which might be involved in the mechanism, not so far investigated in detail, include the role of the septum dividing the two auditory systems, and also the degree of opening of the acoustic spiracles.

Acknowledgements. We thank Professor A. Michelsen and Drs. O. Larsen and R. Kühne for critical reading of an early version of the manuscript.

References

Bailey WJ, Thomson P (1977) Acoustic orientation in the cricket *Teleogryllus oceanicus* (Le Guillou). J Exp Biol 67:61–75

Boyan GS (1979) Directional responses to sound in the central nervous system of the cricket *Teleogryllus commodus* (Orthoptera, Gryllidae). I. Ascending interneurons. J Comp Physiol 130:137–150

Coles RB, Lewis DB, Hill KG, Hutchings ME, Gower DM (1980) Directional hearing in the Japanese Quail (*Coturnix coturnix japonica*). II. Cochlear physiology. J Exp Biol 86:153–170

Eibl E, Huber F (1979) Central projections of tibial sensory fibres within the three thoracic ganglia of crickets (*Gryllus campestris* L., *Gryllus bimaculatus* DeGeer). Zoomorphologie 92:1–17

Esch H, Huber F, Wohlers DW (1980) Primary auditory neurons in crickets: physiology and central projections. J Comp Physiol 143:129–134

Feng AS, Shofner WP (1981) Peripheral basis of sound localization in anurans. Acoustic properties of the frog's ear. Hearing Res 5:201–216

Hill KG (1974) Carrier frequency as a factor in phonotactic behaviour of female crickets (*Teleogryllus commodus*). J Comp Physiol 93:7–18

Hill KG, Boyan GS (1976) Directional hearing in crickets. Nature 262:390–391

Hill KG, Boyan GS (1977) Sensitivity to frequency and direction of sound in the auditory system of crickets (Gryllidae). J Comp Physiol 121:79–97

Hoy RR, Paul RC (1973) Genetic control of song specificity in crickets. Science 180:82–83

Hutchings ME, Lewis DB (1981) Response characteristics of primary auditory fibres in the cricket *Teleogryllus oceanicus*. J Comp Physiol 143:129–134

Kleindienst HU, Koch UT, Wohlers DW (1981) Analysis of the cricket auditory system by acoustic stimulation using a closed sound field. J Comp Physiol 141:283–296

Larsen O (1981) Mechanical time resolution in some insect ears. II. Impulse sound transmission in acoustic tracheal tubes. J Comp Physiol 143:297–304

Larsen ON, Michelsen A (1978) Biophysics of the ensiferan ear. III. The cricket ear as a four-input system. J Comp Physiol 123:217–227

Michel K (1974) Das Tympanalorgan von *Gryllus bimaculatus* DeGeer (Saltatoria, Gryllidae). Z Morphol Tiere 77:285–315

Mörchen A, Rheinlaender J, Schwartzkopff J (1978) Latency shift in insect auditory nerve fibres: a neural time cue of sound direction. Naturwissenschaften 54:656

Murphey RK, Zaretsky P (1972) Orientation to calling song by female crickets, *Scapsipedus marginatus* (Gryllidae). J Exp Biol 56:335–352

Nocke H (1972) Physiological aspects of sound communication in crickets (*Gryllus campestris* L.). J Comp Physiol 80:141–162

Popov AV, Shuvalov VF (1974) Spectrum, intensity and directional characteristics of the calling song emission in the cricket *Gryllus campestris* under natural conditions. (In Russian) J Evol Biochem Physiol 10:72–80

Rheinlaender J, Blatgen G (1982) The precision of auditory lateralization in the cricket *Gryllus bimaculatus*. Physiol Entomol 7:209–218

Stephen RO, Bailey WJ (1982) Bioacoustics of the ear of the bushcricket *Hemisaga* (Sagenae). J Acoust Soc Am 72:13–25

Taylor M (1978) Trapezoidal waveform generator. New Electronics 11:20–21

Thorson J, Weber T, Huber F (1982) Auditory behaviour of the cricket. II. Simplicity of calling song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. J Comp Physiol 146:361–378

Wendler G, Dambach M, Schmitz B, Scharstein H (1980) Analysis of acoustic orientation behaviour in crickets (*Gryllus campestris* L.). Naturwissenschaften 67:99–100

Young D, Ball E (1974) Structure and development of the auditory system in the prothoracic leg of the cricket *Teleogryllus commodus* (Walker). I. Adult structure. Z Zellforsch 147:293–312

Zhantiev RD, Kalinkina IN, Chukanov VS (1975) The characteristics of the directional sensitivity of tympanal organs in *Gryllus bimaculatus* De Geer (Orthoptera, Gryllidae). Entomol Obozr 54:249–257