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Interaural intensity and time discrimination in an unrestraint grasshopper: a tentative behavioural approach*

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Summary. An experimental paradigm is introduced to determine minimal interaural intensity and time differences used as cues for the lateralization behaviour of the male grasshopper, *Chorthippus biguttulus*. By presenting synthetic female sound via two miniature, bilaterally arranged speakers a quasi-dichotic stimulus situation could be achieved under predictable error estimations (Fig. 1).

(1) The resolution of the grasshopper's auditory system for interaural intensity differences is about 1–2 dB (Figs. 3, 4). At intensity differences above 1.6 dB turns towards the 'leading side' are performed without any error, the 75% (resp. 25%) threshold of correct choice is achieved at 0.6 dB. The response characteristics also document the high degree of conformity between the animals and the degree of individual auditory handedness which was found to be maximally 1 dB.

(2) The resolution for interaural time differences (at equal sound intensities on both sides) is of the order of 1.0 ms (Fig. 5). The 75% (resp. 25%) threshold of correct choice is achieved at 0.4 ms.

Introduction

For orthopteran insects there are many reports about the precision and general performance of sound localization (see e.g. Murphey and Zaretsky 1972; Oldfield 1980; Weber et al. 1981; Thorson et al. 1982; Schmitz et al. 1982; Rheinlaender and Blätgen 1982; Latimer and Lewis 1986). However, there is very little information available about the minimum interaural cues involved, such as sound intensity or time differences. One of the reasons is that in insects body size, and hence the interaural disparity, is minute, whis impairs the application of e.g. head phones for independent ear stimulation. Moreover, in cricket and grasshopper species the two hearing organs are acoustically coupled by means of complex tracheal structures (for reviews, see Michelsen and Nocke 1974; Hill and Boyan 1977; Michelsen 1979; Lewis 1983). On the other hand, most insect species exhibit directional information only during walking, (or even during flight) which is a further disadvantage for the design of a dichotic stimulation experiment. Thus, our present behaviourally defined knowledge of thresholds between interaural intensities and time differences is exclusively derived from psychoacoustic studies on humans (reviewed by Mills 1972; Blauert 1974; Jeffress 1975) and on some vertebrate species such as cats (Wakeford and Robinson 1974), monkeys (Houben and Gourevitch 1979) and the barn owl (Konishi 1983).

This study presents a first attempt to determine behaviourally minimum interaural cues for the lateralization process in the auditory system of an insect. We take advantage of the rather elaborate acoustic communication system between males and females of the acridid species *Chorthippus biguttulus*. In this species (as in related ones) pair formation is achieved by duetting in which the male's song elicits an acoustic reply from the receptive female to which the male then reacts phonotactically. The orienting turn is followed by a short forward movement in the new direction after which the male initiates the next alternating song, finally

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approaching the female in a series of such sequences of behaviour (von Helversen 1972; von Helversen and von Helversen 1983). Thus the phonotactic procedure of the male is characterized by distinct stops and singing, followed by just as distinct turns towards the sound source on the basis of a simple right-left discrimination (Rheinlaender et al., unpublished).

At these stops we presented the sound stimulus via two bilaterally arranged speakers and thus achieved a quasi-dichotic stimulus situation under predictable error estimations. Thus the effects of interaural cues can be studied in a behavioural experiment and compared with those known from higher vertebrates.

Materials and methods

A total of about 50 grasshopper males of the acridid species *Chorthippus biguttulus* L. was used for the experiments. They had been caught as imagines between August and October in field locations near Erlangen and Freiburg, FRG.

Experimental procedures. The experiments were performed in a reflection-attenuating room (area 2×2 m^2) lined with foam prisms. The animal under test was placed on a round, cloth-covered table-top (70 cm in diameter) raised about 90 cm above the ground in the centre of the chamber to provide free access for the experimenter to the insect. Thus, before each phonotactic turn, a pair of miniature speakers could be positioned towards the insect with high precision as shown schematically in Fig. 1A. The two transducers were fixed to an U-shaped frame, so that for each position of the male the two speakers could be placed equidistantly (20cm) from the two hearing organs. With a needle pointing along the longitudinal body axis on to the abdomen, in general, the aligning was achieved with an accuracy of about 1 mm. The table was illuminated by a 25 W red light bulb, so that any visual information for the animal was reduced to a minimum. Air temperature inside the chamber was maintained between 29 °C and 32 °C.

Whenever the male began to sing spontaneously, one synthetic female sound was broadcast with a delay of a few seconds via the pair of speakers, and the turning of the male to right or left was noted and evaluated as a response. Very rarely did the animals fail to perform a turn, either by jumping straight forward or by exhibiting no locomotory response at all, which mainly occurred when the two sounds were simultaneous and of equal intensity (thus simulating a speaker position exactly from behind or in front of the animal). These few results were discarded as they provided no information about the auditory lateralization capacity of the animal.

After some practice we succeeded in re-arranging the speaker device in time for the next sequence of behaviour. By frequently changing the 'leading stimulus' from one side to the other we could also influence the directions of the turns and thus avoid habituation and fatigue of the motor system underlying turning behaviour. By this method we also controlled the pathway of the insect, so that tracking in the middle (and not along the edges) of the table-top could be achieved without touching the insect. Sequences of phonotactic turns were repeated until the male stopped turning and singing, which for highly motivated animals usually occurred after 10–30 exchanges. Normally the male then resumed singing after about 1 min for a similar period of time, so that about 100–200 tests could be repeated without fatiguing of the insect. In general motivation was restored on the following days.

For generating the sound stimuli we used a digitally stored (Digital Equipment, PDP12, for methods see Dörrscheidt and Rheinlaender 1980) natural female song consisting of a comparatively broad spectrum (ca. 2–12 kHz) with a main peak between 5 and 7 kHz. This model song (lasting for about 1 s) was copied with equal amplitudes on two (direct) channels of a magnetic tape recorder (Racal Store 4 DS, speed 7 1/2 inch/s) with time differences from 0 up to 4 ms in steps of 0.5 ms. As the computer was provided with one DA converter only, the recording had to be performed in two successive procedures. This resulted in a time shift of up to ± 50 µs between the two signals. Thus the degree of coherence of the two sound signals should be considerably reduced.

The two signals were amplified by a custom made two channel amplifier, the intensity of each channel being independently variable in 1 dB steps, and broadcast via two headphone transducers (AKG acoustics, type DKC 29/51). The overall frequency response of the stimulation unit was flat within ± 3 dB from 500 Hz up to 12 kHz, thus encompassing the essential acoustic spectrum of the natural stridulatory sound of the female.

Intensity measurement and calibration. The sound intensity of the stimulus was measured at the position of the animal (see Fig. 1A) with an accuracy of about 2 dB using a Brüel & Kjaer system (microphone 4133, measuring amplifier 2606). The stridulatory sounds of both *Chorthippus biguttulus* males and females are strongly amplitude-modulated signals often performed with increasing intensity during a single chirp which complicates the precise intensity calibration of such signals. This is true particularly when the sound signal is composed of a spectrum instead of a single sine wave. The values in this work are given in peak readings (re 20 µPa).

It is of great importance to define the point of equal loudness of the two speakers as accurately as possible. As any two speakers show at least minute differences in the frequency spectrum which might be differently weighted by the auditory system of the grasshopper and the measuring equipment with a linear frequency characteristic, we decided to use the auditory system of the animals themselves as a 'zero detecting device'. We defined the point of symmetry between the pair of speakers used (at absolute sound intensities between 54–58 dB SPL) by increasing and decreasing in 1 dB steps the sound intensity in one speaker while keeping the intensity of the other speaker constant (time difference between the two signals 0 ms). To exclude the effect of interaural handedness, the speakers were also switched to the other side of the body by twisting the frame and then the same testing procedure was repeated (see Results). The intensity values between the two speakers with a turning tendency closest to 50% (equal turns to either side) were defined as the point of symmetry (interaural difference 0 dB, see e.g. Fig. 3). As this value did not alter in principle both for several animals and for higher absolute sound intensities we are confident of this definition.

Estimation of error and correction of intensity differences. An intensity difference adjusted at the speakers does not accord with the intensity difference actually stimulating the tympanal membranes, but is less. For calculating this actual difference in intensity it is necessary to know the reduction of sensitivity for ipsi- and contralateral stimulation. Therefore the directional characteristics of the tympanal organ from 5 *Chorthippus biguttulus* males stimulated with the same tape recorded signal as used in the behavioural experiments were measured electro-

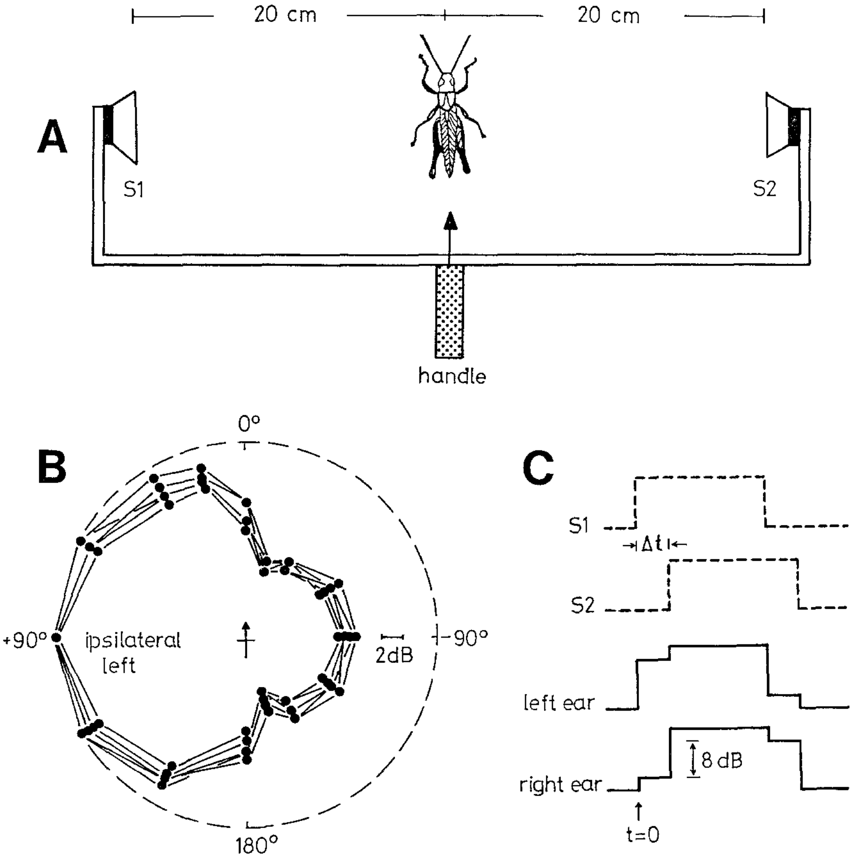

Fig. 1. A Speaker arrangement for the application of a quasi-dichotic stimulus situation to a *Chorthippus biguttulus* male (grasshopper not in scale).
B Directional characteristics of the tympanal organ of 5 *Chorthippus biguttulus* males stimulated with the same synthetic female sound as used in the behavioural experiments.
C Illustration of the temporal superposition of two rectangularly modulated sound signals at equal sound intensities but with a time difference Δt between both speakers (for further explanations see text)

physiologically. These results are based on multi-unit recordings of the activity of the tympanal nerve with a KCl-filled glass micropipettes (input resistance 5 MΩ) and thus providing reliable means of measuring the lowest sensitivity of the organ. The recording site was close to the entrance of the tympanal nerve within the metathoracic ganglion. The ganglion was penetrated by an electrode from the ventral side; care was taken not to interfere with the interaural tracheal system. Tympanal threshold was defined as the lowest level of sound intensity at which the nervous response monitored by headphones was just above 'hearing threshold' of the experimenter. Measurements were performed with an accuracy of ± 1 dB (for further details of the recording apparatus see Rheinlaender and Römer 1980).

The directional curves in Fig. 1B show that the reduction of sensitivity between 90 ° ipsilateral and 90 ° contralateral is of the order of 8 dB which is in agreement with the values obtained in behavioural experiments with unilaterally deaf animals (von Helversen 1984) and neurophysiological recordings in freely moving *Chorthippus biguttulus* (Wolf 1986). Therefore, to evaluate the actual intensity at each ear the power of the contralateral sound stimulus attenuated by 8 dB has to be added to the ipsilateral stimulus. Thus, an intensity difference of 1, 2 or 3 dB etc. adjusted between the two speakers results in an effective interaural difference of 0.8, 1.5, 2.2 dB etc., which is documented in the abscissa of Figs. 3 and 4. In our results we refer to these latter values. Of course, this estimation is correct for incoherent sound sources, only. To test whether our signals caused the same intensity differences as did independent sound sources, we also measured several intensity discrimination curves using artificial stimuli consisting of amplitude modulated, but incoherent noise. As such curves showed the same steepness, we are confident, that for the animal the perceived intensity difference was the same irrespective of the type of signal and that the – possibly persisting – degree of coherence (see above) had no influence on the perceived intensity difference.

Consequently, when presenting interaural time differences only, the 'cross-talk' between the two ears also influences the time course of the effective signal shown schematically in Fig. 1C. The dashed lines indicate the time courses of a rectangularly modulated signal at the two speakers with equal amplitudes and speaker S1 leading in time. As each signal from the opposite side is attenuated by about 8 dB, the resulting sound signal can be approximated as a function of the direct and attenuated sound wave, as shown by the dark lines of Fig. 1C. The resulting signals at the two ears are rather distorted and in the example given the right tympanal membrane also is stimulated at the time $t=0$, of course by a signal attenuated by 8 dB rel. to the left side. However, from neurophysiological measurements on single receptor fibres we know that this should be unimportant, as for all receptors not yet saturated an intensity decrease by 8 dB causes an increase of response latency of several milliseconds (for details see Mörchen et al. 1978; Römer 1976). Therefore, we can be sure that the *onset* of neural excitation on each side is in fact caused by the loudspeaker on that side. So these cross-talk effects can be assumed to be inefficient and will not be considered further in this study.

Results

When properly motivated, *Chorthippus biguttulus* males respond to the female's song with a prompt

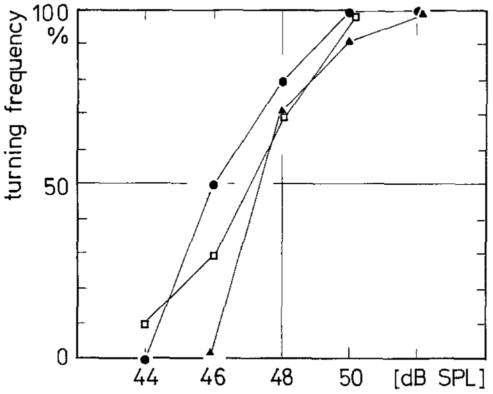

Fig. 2. Intensity characteristic of turning behaviour of 3 *Chorthippus biguttulus* males unilaterally stimulated with a synthetic female sound. Starting with low stimuli, the intensity was increased in steps of 2 dB and this procedure repeated at least ten times for each animal

turn towards the sound source. This orientation movement occurs very reliably as it is incorporated in a rather stereotyped behavioural pattern which is set going by the male's own song.

Figure 2 shows sample curves of the probability of eliciting a phonotactic turn at different sound intensities. In contrast to the following experiments, only one speaker (on right or left) was active in this case. The response characteristics are rather steep and they saturate within 6–8 dB above that intensity value where a first turning response was elicited at all. For each animal we noted the lowest sound intensity at which the response level was 90% or better. In all experiments the bilateral stimulation was performed 4 dB above this individual 90% threshold. Thus we were sure that both auditory sides were activated well above hearing threshold.

Before considering the more general results, we will first demonstrate the behaviour of two animals exhibiting a significant auditory handedness when stimulated with interaural intensity differences. In Fig. 3, the filled symbols represent the response with the speaker S1 on the right body side; for the open symbols speaker S1 was on the left side.

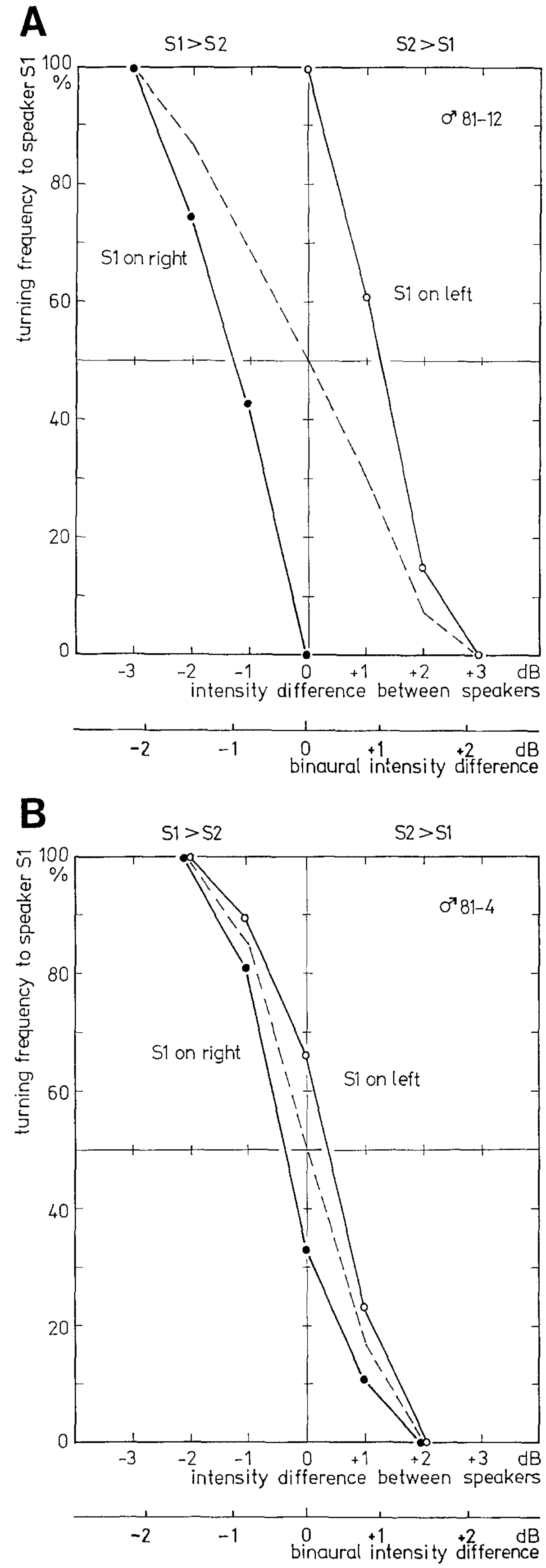

Fig. 3 A, B. Auditory lateralization (turning tendency to speaker S1 in % of all turns) as a function of interaural intensity differences in two *Chorthippus biguttulus* males. The results in **A** and **B** document different degrees of auditory handedness ($n =$ 20–30 turns/data point). Note that the broken lines (representing the averaged responses for the two speaker configurations) precisely cross the zero point of the coordinate system, thus confirming the symmetry of the stimulation system. For further explanations see text

It is evident, that with equal intensities at both ears (interaural intensity difference 0 dB) the two animals did not turn with equal probability to either side (as would be expected for a non-handed animal). In contrast, both individuals preferred turning to the left. Shifting the speaker S1 from the right to the left body side resulted in a parallel shift of the curves along the horizontal axis (Fig. 3, open symbols). This indicates that they were more sensitive on the left auditory side. The amount of this shift indicates the magnitude of auditory handedness for each subject. The most pronounced asymmetry observed was about 1 dB as exemplified in Fig. 3A.

It should be noted that averaging each pair of curves (by evaluating the turns regardless of the position of the speakers) resulted in each case in a curve which precisely crossed the zero point of the coordinate system (see Fig. 3A, B dotted lines). Thus there was no asymmetry in the stimulating system. Asymmetry in the motorsystem of the animals, which also occurred in some cases, resulted in an asymmetrical steepness of the reaction curve: As long as the louder speaker was on the side to which the animal tended to turn, its turns to this side were facilitated already by slight intensity advantages. When the sensory input was equal on both sides the motor asymmetry prevailed, whereas the curves became less steep when the sensory input had to work against the turning preference. In contrast to sensory asymmetry the handedness of the motor system was reversible. It occurred mainly when the animals became exhausted towards the end of an experiment.

Figure 4 shows the sensitivity of 12 males to interaural intensity differences, systematically tested with speaker S1 on the left side of the body. Two results are remarkable. First, the steepness of the curves is very similar and the curves saturate at intensity differences of 1–2 dB. At these values the animals performed turns to the 'leading ear' without any error which means that these interaural differences must be encoded with high reliability within the CNS. The 75% (resp. 25%) level of correct performance is reached at an intensity difference of 0.6 dB. The ability of the insects to distinguish minute interaural intensity differences is thus of the same order of magnitude as that of vertebrates.

Second, the crossing points of the curves along the horizontal axis are equally distributed about the zero point. They give information about the auditory handedness of each animal (compare with Fig. 3) and reveal that there was no bias in our sample of animals. It is not shown here that for higher sound intensities at both speakers results similar to those documented in Fig. 4 were obtained. This indicates that the precision of auditory lateralization is independent of the general intensity level.

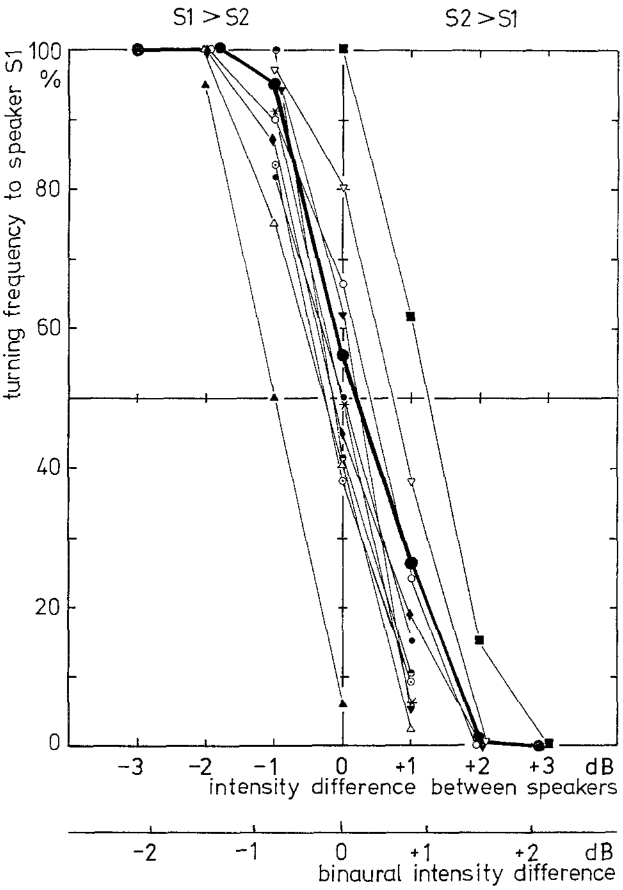

Fig. 4. Auditory lateralization of 12 *Chorthippus biguttulus* males as a function of interaural intensity differences with speaker S1 on left body side ($n = 20$–30 turns/data point). One response characteristic (drawn enhanced) was also measured at saturation levels. Note the high degree of conformity between animals with respect to the steepness of the curves. For further explanations see text

It is well known from neurophysiological studies that the auditory receptors of insects are very sensitive to sound intensity changes and that both spike rate and latency shift of the responses are closely correlated with sound direction (see e.g. Mörchen et al. 1978). Therefore, at the level of the CNS, there are two neuronal codes available: a comparison of spike count and of response latencies between both sides each of which can adequately specify the side of the sound source.

With our behavioural paradigm we can study the effect of the physiological 'time cue' independently from the other cue. Application of equal intensities on both sides will cause an equal excita-

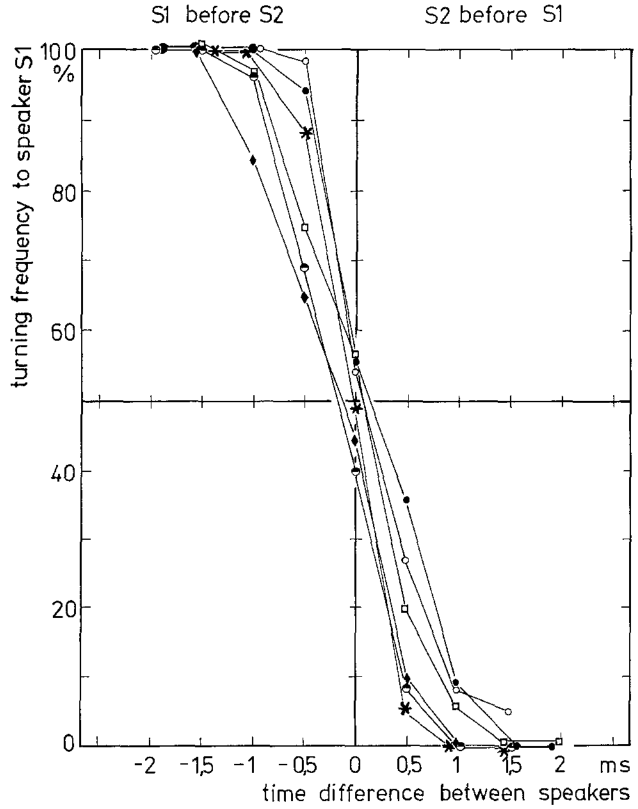

Fig. 5. Auditory lateralization (turning tendency to speaker S1 in % of all turns) of 6 *Chorthippus biguttulus* males as a function of interaural time differences obtained at equal sound intensities on both sides ($n = 20$–62 turns/data point, 10 in one case). For further explanations see text

tion of the tympanal nerves in terms of spike numbers, but a time shift of the pattern between left and right will induce an equivalent latency difference in the grasshoppers CNS. Figure 5 shows that the application of interaural time differences has effects similar to those shown for interaural intensity differences in Figs. 3 and 4. The response characteristics are also very steep and saturate at time differences of about 1.0 ms. Thus, a temporal advantage on one auditory side of the order of 1.5 ms already leads to turns without error to the 'leading side'. The 75% (resp. 25%) level of correct performance is reached at a time difference of 0.4 ms.

Discussion

The applied experimental paradigm allows a first insight into the accuracy of interaural intensity and time discrimination of the auditory system in an insect. The acquisition of this information is facilitated by the robust behavioural pattern of the species investigated (this also seems to be true for other orthopterans, see e.g. Heller and von Helversen 1986; Robinson et al. 1986; Zhantiev and Korsunovskaya 1986). The phonotactic approach of a *Chorthippus biguttulus* male is characterized by sequences of 'stop and go behaviour' in that it sings and orients very reliably towards the acoustic reply of the female during the intervals between periods of forward movement.

Besides the small degree of auditory handedness (see Fig. 3), there is a remarkable sensitivity of *Chorthippus biguttulus* males to interaural intensity differences (Fig. 4). At differences of about 1 dB only the animals turn significantly towards the louder side. This corroborates former estimations of perceived differences in intensity based on the lateralization behaviour of the cricket. These were inferred indirectly by comparing the accuracy of orientation with the directional characteristic of the single ear (Rheinlaender and Blätgen 1982; for similar results obtained in choice experiments see Shuvalov and Popov 1979). Figures 4 and 5 also demonstrate the high level of consistency between the animals. This seems to be a fundamental feature of sound localization behaviour in insects.

Similar values to those shown in Fig. 4 had been obtained from higher vertebrates when optimal sound signals where presented. The threshold for interaural intensity differences lies at 0.5 dB for man (Mills 1958), about 1 dB for the cat and the barn owl (Wakeford and Robinson 1974; Konishi, unpublished results) and about 2–3 dB for monkeys (Wegener 1974; Houben and Gourevitch 1979). Thus, in this respect the capacity of the grasshopper's auditory system resembles that of higher vertebrates.

Referring to the time resolution, the performance of the insect's ear does not compare to the acuity that can be reached by vertebrates (5–40 µs; for review see Blauert 1974). Vertebrates (such as mammals and the barn owl) with comparatively large distances between their ears, use the actual time difference between the incidence of the sound at the two ears to evaluate the direction of it's source. Therefore an enormous evolutionary pressure may have forced their CNS to develop this astonishing accuracy. In contrast, the CNS of insects uses time difference caused by neurophysiological processes, the latency difference originating from different intensities at the two tympanal organs.

At present the physiological processes providing such an acuity of behaviour remain speculative, although there are some converging results. It has been shown that the neural responses recorded from a pair of auditory interneurons in the ventral nerve cord of a bushcricket should provide significant information to discriminate interaural intensity differences of 2–4 dB (Rheinlaender 1984). By assuming parallel processing of several fibres with similar characteristics it is conceivable that the behavioural result may be also achieved. A single auditory receptor exhibits rather steep characteristics of intensity response; this gives a high resolution for intensity, but the curves saturate at about 20 dB above threshold (see e.g. Römer 1976; Miller 1977; Mörchen et al. 1978). Thus the sphere of function concerning intensity discrimination is limited to the dynamic range of the receptor, and several elements of graduated sensitivity would be necessary to cover the whole range of intensities. However, we neither know how many receptors (of about 80 in each organ, Gray 1960) are activated simultaneously when the grasshopper is stimulated by a conspecific sound, nor do we know how accurately different levels of sound intensities are encoded by each receptor. Further, the degree of physiological symmetry between the two organs is unknown (for first physiological analysis in the CNS of crickets and bushcrickets see Boyan 1979; Rheinlaender and Römer 1980). Thus the ability of insects to evaluate such minute interaural differences remains a challenge for future sensory network analysis.

At the receptor level the intensity difference can be encoded in two ways as spike counts and response latencies. There are several neurophysiological indications that both parameters strongly influence directionally sensitive interneurons (Rheinlaender and Mörchen 1979; Kleindienst et al. 1981; Römer and Rheinlaender 1983). By varying interaural time differences only (at equal sound intensities) the sensitivity of the insects to the neuronal time cue can be established directly. Figure 5 shows that the auditory system of *Chorthippus biguttulus* clearly distinguishes time differences of the order of 1 ms in an artificial situation where a spike count could not play a role because the intensity was equal on both sides.

The resolved time difference is well within the range of time shifts in the receptor responses that occur when the tympanal organ is stimulated from different directions (Mörchen et al. 1978; Ronacher, pers. comm.). A similar temporal resolution was found at the level of the CNS (see Fig. 2 in Rheinlaender and Mörchen 1979). Thus, there is both a behavioural and neurophysiological account for the time cue alone being able to affect the synaptic activity of directionally sensitive interneurons.

During the acoustic orientation in the free sound field both cues (spike count and response latency of receptor fibres) probably operate together and may have mutually reinforcing effects. This may explain the pronounced directionality of auditory interneurons observed in several orthopteran families (for review see Boyan 1984; Michelsen and Larsen 1984) and it might explain how the rather simple auditory system of a grasshopper provides a performance equivalent to that of higher vertebrates with respect to binaural intensity discrimination.

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