

Cues for male phonotaxis in the duetting bushcricket *Leptophyes punctatissima*

Uwe Zimmermann¹, Jürgen Rheinlaender¹, and David Robinson²

¹ Lehrstuhl für Allgemeine Zoologie und Neurobiologie, Ruhr-Universität Bochum, D-4630 Bochum, Federal Republic of Germany

² Department of Biology, The Open University, Milton Keynes, MK7 6AA, United Kingdom

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Summary. A computer controlled setup is introduced which allows the song analysis of both male and female *Leptophyes punctatissima* during duetting in a laboratory situation. The essential acoustical parameters for the initiation of the male's phonotactic approach towards the stationary female are described. The female responds 'reflex-like' to the male song after a remarkably short delay time of about 28 ms. The male only performs phonotaxis if he perceives the female reply above an intensity value of about 50 dB SPL and if the female response falls within a critical 'time window' from 25 to a maximum of 55 ms after the onset of his song (Figs. 3 and 5). The sound intensity and overall time delay of the female response can be varied independently, so that the relationship between both parameters and their limitations for maximum phonotaxis distance can be described.

Introduction

In most acoustically communicating orthopteran species the receptive but mute female moves towards the calling but stationary male. This implies that the major intraspecific recognition is made by the female and there are many reports about the auditory cues involved (for recent literature see e.g. Bailey 1985; Doherty 1985; Huber and Thorson 1985; Latimer and Lewis 1986).

In contrast, some acridids and tettigoniids have evolved a more elaborate communication system. Pair formation is achieved by duetting as the male song elicits an acoustic reply from the stationary female to which the male then responds phonotactically (von Helversen 1972; Hartley et al. 1974;

Heller and von Helversen 1986; Zhantiev and Kor-sunovskaya 1986). This duetting, always initiated by the male, involves sound production and recognition in both sexes and there are only a few reports describing the underlying mechanisms (von Helversen and von Helversen 1983; Heller and von Helversen 1986; Robinson et al. 1986).

In the phaneropterine bushcricket *Leptophyes punctatissima* the song durations of male and female are in the order of a few milliseconds and thus both songs are unusually short by comparison with those of most other orthopteran insects. Moreover, the receptive female responds to the single call of a male after a remarkably short delay time of about 28 ms (Robinson et al. 1986) and this delay time is remarkably constant for each individual. Thus *Leptophyes punctatissima* females exhibit one of the fastest acoustico-motor responses known among insects (for comparison see Roeder 1963; Miller 1975; Fullard 1982; Moiseff and Hoy 1983; Heller and von Helversen 1986), and the constancy of the delay can be used by the male as a temporal feature of recognition. In fact, experimental variation of this delay time revealed that the female reply has to fall within a very specific time window from about 20 to 50 ms (relative to the onset of the male song) in order to elicit a phonotactic approach in the male (Robinson et al. 1986). This places a high demand on both the temporal sensitivity and the precision in the acoustic behaviour of both sexes which – in contrast to most orthopterans – seems to be a specific feature that has evolved only in some bushcricket species (Heller and von Helversen 1986).

In *Leptophyes punctatissima* maximum communication distance is limited to a few metres. As this species communicates in the ultrasonic range (centre frequency of the songs at about 40 kHz), the sound attenuation is increased compared to

sonic frequencies (Michelsen and Larsen 1983). The size of the male time window is such that the travelling time of sound through air (about 3 ms/m) becomes a significant fraction of the female delay time as perceived by the male. These limitations make this species particularly suitable for the analysis of the songs and the related phonotactic behaviour under laboratory conditions, using the natural ranges of interindividual distances. By applying a computer controlled recording system the temporal relationships of the duetting pair can be described quantitatively. A further goal of this study is the analysis of maximum phonotaxis distance and the definition of the limiting factors involved.

Materials and methods

Leptophyes punctatissima males and females were obtained as last instars cultured by Dr. J.C. Hartley at the University of Nottingham (for details of culturing see Deura and Hartley 1982). In addition, during the early summer period last instars were collected from wild stock locations close to Bochum and Nordkirchen (the latter being located about 50 km north of Bochum). In order to prevent copulation, the sexes were kept separately after the final moult, but they were not acoustically isolated (except 3 days before an experiment, see below) which kept the females at a high responsive level (see Robinson 1980). The temperature inside the cages varied between 16 and 24 °C, the artificial light was switched on at 06.00 a.m. (LD 14:10 h cycle).

Experimental procedure and quantitative measure of phonotaxis. The behavioural experiments were performed in an anechoic chamber (Grünzweig und Hartmann, reflections <1% for frequencies above 100 Hz). The size of the chamber was sufficient to study a maximum communication distance between a pair up to 7 m. In each trial a single male and female (aged at least 1 week after the final moult) were placed on two separate foam mats suspended at the same height of 1.5 m above the ground of the chamber to exclude the exchange of vibrational information between them. The foam mat of the stationary female had a diameter of about 10 cm and it could be placed at variable distances to the male. The foam mat of the male had a size of 1 × 1 m with the male placed on a wire mesh platform (diameter 18 cm) 2 cm above and in the centre of the mat (see Fig. 1). Locomotory movements of the male on this platform were not considered for behavioural analysis. However, a quantitative measure of male phonotaxis was obtained when the male climbed down the platform and left a circle subdivided into 4 sectors (see dashed line in Fig. 1). Thus, we obtained a test value for the occurrence of phonotaxis on the basis of a four sector analysis.

To eliminate any visual cues that the male might use for orientation, experiments were performed in dim red light with only one bulb (15 W) mounted 60 cm above the centre of the male's platform. The light intensity was just sufficient for the operator to observe the platform exits of the male. The ambient temperature at both the male's and female's platform was checked with two separate probes of a digital thermometer (accuracy ± 0.3 °C) and kept at 28 ± 1 °C.

For the tests we selected only those males that sang spontaneously within the culture cages. Pilot experiments revealed

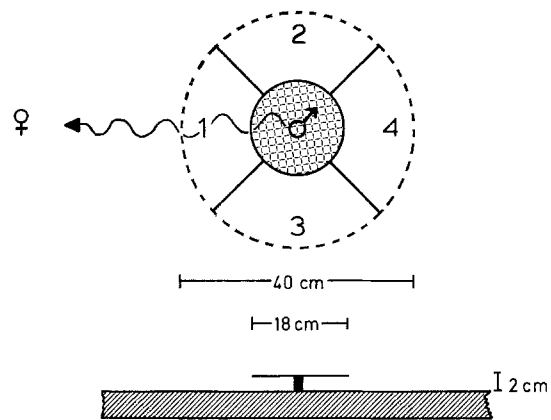


Fig. 1. Top view (above) and side view of the wire mesh platform and the foam mat with indication of the release point of the male and its phonotactic path towards the female. After the male had crossed the circle line (dashed line), it was caught, the chosen sector was protocolled and the male was set back onto the platform for a new phonotactic approach

that females responded to ultrasonic clicks most reliably and over a long time period if they were isolated acoustically from their males for 3 days (see also Robinson 1980). This period of isolation was used for all females tested. Before starting a trial a female which responded to finger nail clicks was selected. Responsive females tend to respond to any brief clicks with components in the ultrasonic range (Hartley and Robinson 1976). Thus we were sure that each test pair was highly motivated for a phonotactic experiment.

In general, the male resumed singing within a few minutes of being placed on the experimental platform. Most of the females responded promptly when being confronted with the male's song and they remained responsive for several hours. Only 18% of the females lost their motivation to respond to each of the male songs after a few minutes of testing. These trials were aborted and discarded.

In most cases the male started phonotaxis as soon as it received the female reply from a close distance and in general it continued its singing and phonotactic approaches for several hours. As soon as it had crossed the border line of the testing circle (see Fig. 1), it was caught and placed back onto the centre platform in order to start a new approach. Each border crossing of a chosen sector was input into a computer system (see below) in order to calculate online whether the male left the circle at random or with significant preference ($P_2 < 0.05$) of sector 1 pointing in the female's direction. The distribution of circle exits was tested against the null hypothesis that all sectors would be chosen with the same frequency using a Chi-square test (beginning at $N=16$). If the male tended to choose the 'correct' sector 1 with high reliability (which means that it started its phonotactic approach rather accurately), a Dixon and Mood Sign Test was used in testing the exits of sector 1 against the sum of the other 'wrong' sectors. Thus a significant result ($P_2 < 0.05$) could be obtained with a smaller sample size (starting at $N=6$) compared with the Chi-Square test. In the case of random exits a trial was terminated if a 'wrong' sector was preferred to the 'correct' one and after at least 8 circle exits. In general in the case of positive phonotaxis a trial lasted on average 19 min ($N=49$) and in the case of random circle exits (no phonotaxis) on average 25 min ($N=43$). If a male produced more than 600 calls without leaving the circle this trial was terminated and scored as no phonotaxis. All state-

ments in this paper concerning phonotaxis are based on these statistical calculations. With highly motivated pairs in one session a maximum of 10 tests could be obtained.

Sound recording and analysis. During the experiments the sound of the male was recorded by a Brüel & Kjaer 1/4" microphone (amplifier Brüel & Kjaer type 2604), which was placed 40 cm above the centre of the platform. The female sound was recorded by a Brüel & Kjaer 1/2" microphone (amplifier Brüel & Kjaer type 2606) positioned 30 cm in front of the female but 10 cm below the direct sound path between the pair. Both sound recordings were displayed on a digital storage oscilloscope (Yuko VKS 22-16) and transmitted to a microcomputer (Tandy TRS-80 Model 4p). For each male song and female reply the number of syllables per chirp, the chirp duration and sound intensity were measured online. Furthermore, the chirp repetition rate of the male, the response rate of the female and the latency of her reply relative to the onset of the male song were calculated and displayed online. Sound level values are given in dB SPL (RMS peak readings, re 20 μ Pa).

Analysis of limiting factors of phonotaxis. From the view-point of the male there are two important parameters limiting maximum phonotaxis distance. One is the sound intensity of the female perceived by the male. The other is the overall time delay between the onset of the male song and the female reply. Both the response time and the intensity of her response will vary with her distance from him. Since perceived intensity by the male will depend on the attenuation of sound with distance, and perceived latency will depend on the female's response delay and the travelling time of sound, there exists a given relationship between latency and sound intensity of the female reply. This relationship holds good for a specific female and specific environmental conditions.

To determine the relationship between these measures a second type of experiment was performed, one in which the female was replaced by an electronic device feeding a piezoelectric transducer (RS Components, type 307-351). This type of speaker has a diameter of about 1 cm, providing a sound source comparable in size to a female. The broadcast synthetic signal had a duration of 2 ms and a carrier frequency of 40 kHz. Control trials which compared synthetic with real female signals revealed that the synthetic female signal was an adequate stimulus for the male. With this kind of equipment both the sound intensity and the delay time of synthetic female calls broadcast from the speaker could be varied independently from each other. Thus we were able to define quantitatively how the parameters are combined and which one ultimately limits maximum phonotaxis distance.

Results

In most orthopteran insects the stridulatory sounds are composed of series of pulses lasting between about 100 ms and several seconds. However, this is not the case in some phaneropterine bushcricket species (Heller and von Helversen 1986), and the species *Leptophyes punctatissima* exhibits one of the shortest sounds known. In both male and female a single sound pulse lasts for about 200 to 500 μ s only (see Fig. 2A and B). The male song consists of a series of 3 to 9 pulses with a repetition rate of about 600 Hz, resulting in a

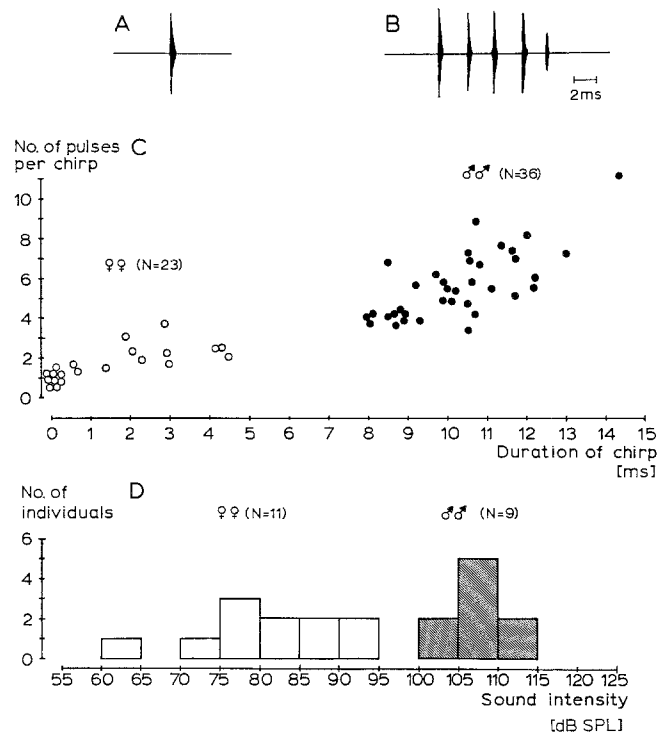


Fig. 2. Oscillograms of a male song (B) and a female reply (A). C Relationship between the duration of a chirp and the number of pulses per chirp for both males and females. D The distribution of sound intensities of both types of signals measured at a distance of 10 cm to the singer. Note that the female sounds are remarkably less loud with a broader distribution than that of the males

total song duration from about 8 to 13 ms (Fig. 2C). The female reply is even briefer (Fig. 2A and C). From the 23 females tested 11 responded in most replies with one pulse only (mean number of pulses per individual between 1.0 and 1.3). 5 females responded with mostly 2 pulses (mean between 1.5 and 1.9) and the remaining ones with two or more pulses per reply showing a somewhat increased repetition rate (800 Hz, mean number of pulses per individual between 2.0 and 3.7, $N=7$) compared to that of the male. Thus, the duration of the female replies strongly differed between individuals and lasted from a fraction of one up to several milliseconds.

The intensities of male and female sounds represent a further sexual dimorphism. The male sound has a median intensity of about 110 dB SPL and is about 25 dB louder than the median of the female replies both measured at a distance of 10 cm (Fig. 2D).

In this study we have analysed the behaviour of a total of 18 communicating pairs with particular emphasis on the study of maximum phonotaxis distance. Figure 3 shows one typical example of

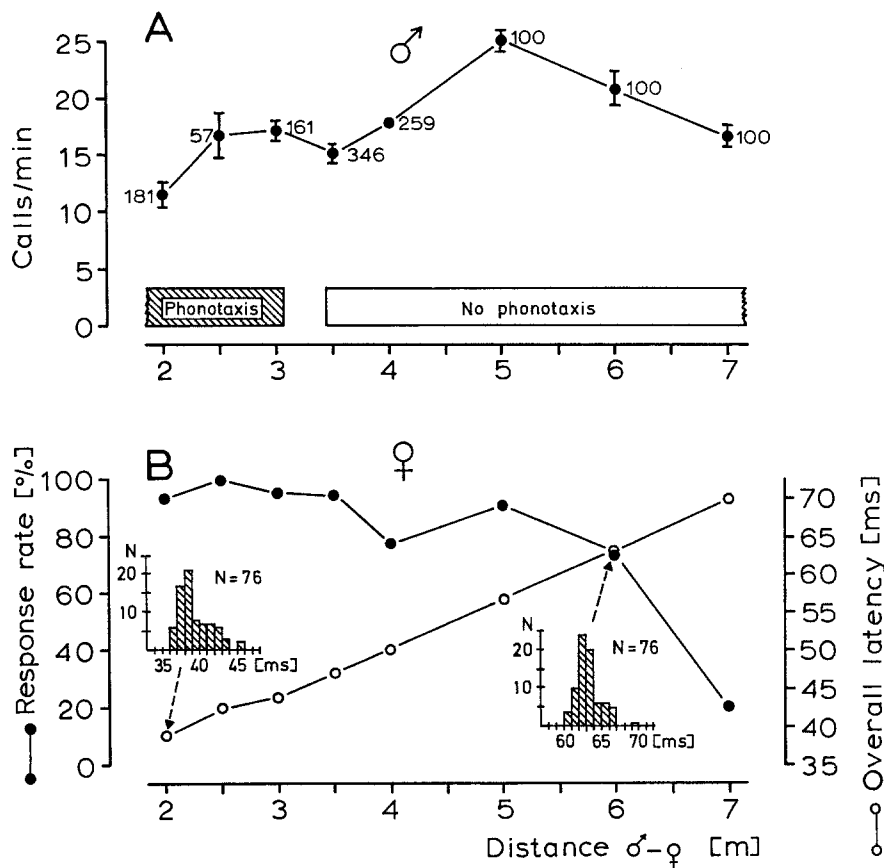


Fig. 3A, B. Sound parameters of a duetting pair at 8 different distances (varied from 2 to 7 m in increments of 0.5 and 1 m) and analysis of the occurrence of male phonotaxis. **A** The mean singing rate of the male is plotted against the male-female distance, vertical bars: SD. Numbers denote the total number of songs per trial. Horizontal bars indicate whether the male performed phonotaxis towards the female significantly. **B** The response rate of the female reply (closed circles) and her overall latency (open circles) with mean values plotted against distance. Insets at 2 and 6 m represent the distribution of response latencies at each distance ($N=76$)

a duetting pair. One important result for this pair is that phonotaxis distance is limited to 3 m; a distance increase of 0.5 m leads to the cessation of male phonotaxis. This cannot be explained by changes in the male singing rate since it was more or less independent of communication distance and fluctuated between 10 and 25 calls per minute (Fig. 3A). The response rate of the female reply does not serve as a limiting factor either as it remains fairly constant and above a level of 75%, even up to a distance of 6 m (Fig. 3B). It demonstrates that this female was highly motivated to attract a male as for each male call there is a high probability of a time-locked female response.

In a previous paper (Robinson et al. 1986) it has been stated that the time delay of the female reply perceived by the male is a critical factor for male phonotaxis. Figure 3B gives a detailed analysis of this overall latency consisting of the travelling time of sound from the male to the female, her net response delay and the travelling time of her reply back to the male. The overall latency clearly increases linearly with communication distance from 37 ms at 2 m up to 68 ms at 7 m due to the increased distance between the pair.

However, it should be recalled that the male performs phonotaxis up to a distance of 3 m only (see Fig. 3A). The increase in distance from 3 to 3.5 m resulted in an increase in time delay from about 44 to 47 ms. If the time delay of the female reply is critical, this increase of only 3 ms has to be recognized by the male as it should exceed the time window. This hypothesis is corroborated by the accurate timing of the female reply, demonstrated by the distributions of the overall latencies at 2 and 6 m (see insets in Fig. 3B). It is noteworthy that the distributions of the delay times are very similar in the two examples. Independent of communication distance the variation of response time is so small that the S.D. are both less than 2 ms (at 2 m: mean overall latency = 38.6 ms, SD = 1.9 ms, $N=76$; at 6 m: mean overall latency = 63.5 ms, SD = 1.6 ms, $N=76$).

On the other hand, if the reduction of sound intensity of the female reply from 3 to 3.5 m is critical, the male must be able to recognize the decrease in sound from 52 to 50 dB SPL as measured at the male's position. The relationship between the two parameters time and intensity will be investigated further (see below).

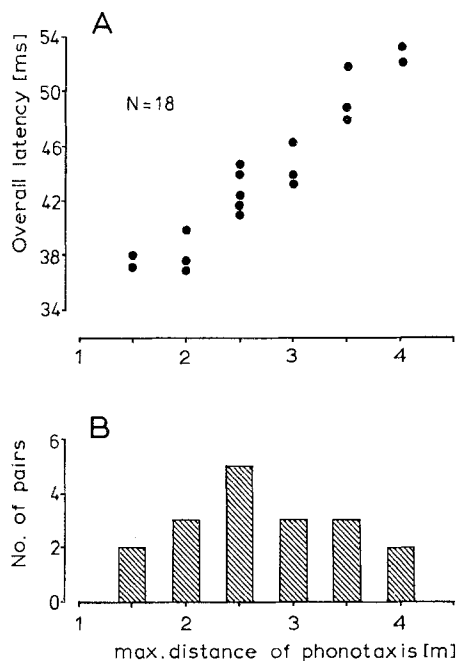
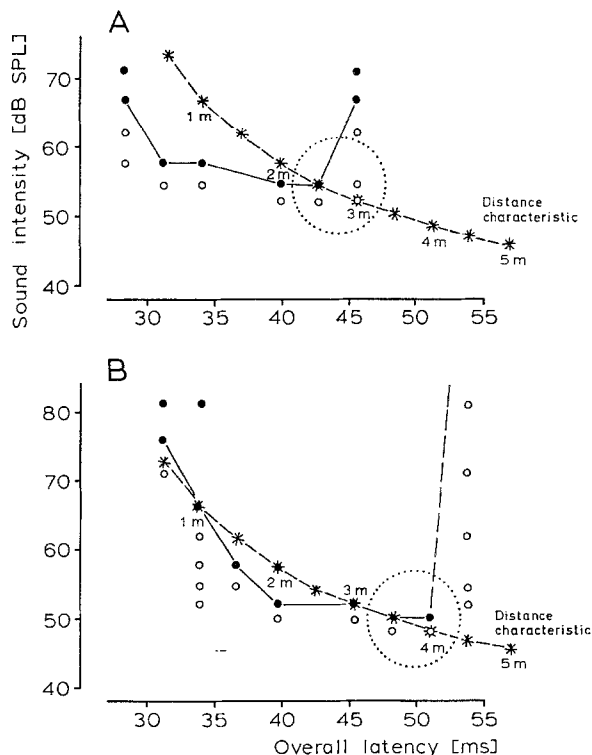


Fig. 4. Distribution of maximum phonotaxis distances of 18 different pairs (**B**) and the corresponding overall latencies at that distance as perceived by the male (**A**)

Figure 4 shows the accumulated data of 18 pairs analyzed in the same way as shown in Fig. 3. The maximum phonotaxis distance varied from 1.5 m to 4 m with a peak at 2.5 m (Fig. 4B). For each pair further increasing the distance by 0.5 m resulted in the cessation of male phonotaxis. In Fig. 4A the corresponding overall latencies of the female replies are plotted against the maximum phonotaxis distance of each pair. The individual overall latencies ranged from 37 to 53 ms, and again there is a linear relationship between the increase of distance and the increase of the overall latency. However, the increase in time cannot be explained by the variation of the net delay of the corresponding female. Statistical analysis revealed that the interindividual variation as expressed by the standard deviation is very small (mean = 28.4 ms, SD = 2.2 ms, N = 18). Also the different individual sound intensities of the female replies could not be correlated with maximum communication distance. Therefore the different maximum communication distances must be ascribed to the specific behavioural properties of the single male such as variation in behavioural hearing threshold and its temporal sensitivity.

In a second type of experiment we replaced a live female by an electronic device in order to vary the sound intensity of a synthetic reply independently of the delay time. Thus we were able to distinguish whether sound intensity or overall latency is the limiting factor for maximum phono-



Limitations at maximal phonotaxis distance

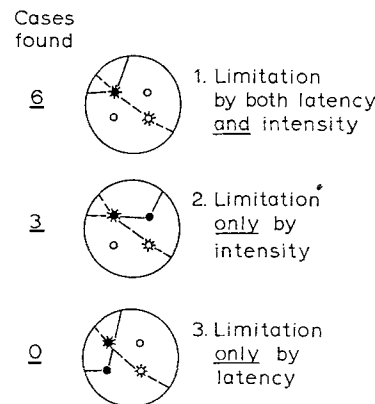


Fig. 5. Threshold curves for phonotaxis of two individual males (solid lines in **A** and **B**) measured with a synthetic female reply. Sound intensity and response latency are varied independently from each other. Closed circles denote positive phonotaxis, open circles no phonotaxis. The distance characteristic (dashed line) is the curve that connects the combinations of sound intensity and overall latency of an average female at specific virtual distances (asterisks). The critical section of cessation of phonotaxis is marked by a dotted circle. The lower part of the figure shows the 3 possible cases of limitation and the number of males found in each case

taxis distance. Specimen results for two males out of a sample of 9 are shown in Fig. 5. The solid line denotes the behavioural threshold curve found for each male. For the male in Fig. 5A the lowest behavioural threshold of 55 dB SPL was found at

an overall latency between 40 and 43 ms. A further increase of response delay by 3 ms only led to an increase in behavioural threshold of at least 10 dB. This increase is even more pronounced in the male of Fig. 5B. For this male the lowest behavioural threshold was 50 dB SPL at response latencies between 48 and 51 ms. A further increase in latency of 3 ms stopped phonotactic behaviour and there was no intensity value in the physiological range which would reinitiate phonotaxis. Similar observations were found in two other males whose results are not shown here, so that in these 3 cases (out of 9) the upper limit of the time window was independent of sound intensity.

The distance characteristic of a mean female is given in Fig. 5 for comparison with the behavioural threshold of the two males. The characteristic (see dashed line with asterisks) is based on sound measurements of 8 females and on a net latency of 28 ms. It represents for an average female the relationship between intensity and overall response latency over communication distance. In Fig. 5A this distance characteristic intercepts the behavioural threshold curve at 2.5 m indicating the 'maximum phonotaxis distance' of this male with the synthetic female. This can be confirmed by taking the time-intensity configuration of 3 m distance where the male did not perform phonotaxis. Independent readjustment of the two parameters to the former value of the 2.5 m distance revealed that only the combination of both values was effective in reinitiating phonotaxis. A similar result was found in 5 further cases indicating that maximum phonotaxis distance had been limited by both parameters, sound intensity and overall latency. In 3 cases the increase of the corresponding intensity value alone led to the reinitiation of phonotaxis which is shown in detail in Fig. 5B. No case was found in which the response delay was the only limiting factor.

From these 9 trials between males and synthetic females we can conclude that in 2/3rd of the cases sound intensity and overall latency were both limiting factors of maximum phonotaxis distance. In 1/3rd of the cases, however, the limiting factor was sound intensity alone. It should be noted that in no case was maximum phonotaxis distance limited solely by the overall latency.

Discussion

The acoustic behaviour of *Leptophyes punctatissima* presents a number of unusual features. Most orthopteran males produce a proclamation

song that indicates their willingness to mate, identifies their species and acts as a signal that the female can localize and move towards. The male remains unaware of the effectiveness of his song until a late stage in the female's phonotactic approach to him. He is, essentially, a speculative singer.

Duetting between male and female is a more elaborate communication system found in some acridids (von Helversen 1972) and bushcricket species (Spooner 1968; Hartley and Robinson 1976; Heller and von Helversen 1986; Zhantiev and Korsunovskaya 1986). It ensures that the male and female remain in acoustic interaction throughout a phonotactic approach. In the behaviour of *Leptophyes* this interaction that has evolved is very fast. The time delay of the female reply (about 28 ms, see below) must be close to the limits of her nervous system. It is one of the shortest acoustico-motor responses yet known (Robinson et al. 1986). That this speed is of importance is made very clear by the temporal sensitivity of the male. Unless the female response falls within the male's 'time window of expectation', he does not perform phonotaxis (Figs. 3 and 4).

In principle, this sensitivity to the timing of the female reply is found in males of other classes of arthropods, and also in other communication systems. Male fireflies (*Photinus*) flash as they fly seeking mates at night. The females flash answers from the ground (Lloyd 1981). The calls of male tick-tock cicadas are answered by the female flicking her wings, which produces a single short sound. This reply has a remarkably uniform time delay of 70–85 ms (Gwynne 1987). Vibratory signals generated by an alder fly male (Rupprecht 1975) and a wandering spider male (Rovner and Barth 1981; Schüch and Barth 1985) have been observed to elicit answering pulses from their receptive female. However, the precise timing shown by the female *Leptophyes punctatissima* and the sharply tuned time window of the male are outstanding in comparison with the other examples known.

Phonotaxis by male *Leptophyes* in the laboratory is prompt and reliable if a minimum set of parameters are fulfilled. Providing that a calling male receives either a reply from a female or a synthetic reply at the right frequency, of short duration and within its time window he will perform phonotaxis. Because the male is so reliable it has been possible to use a statistical method for defining phonotaxis. This method of recording phonotaxis is objective and is an improvement on previous behavioural observations. Coupled with the small size of the insect (and hence the high carrier frequency of the

signal) and relatively small communication distance, this method enabled us to study, for the first time, acoustic communication and pair formation quantitatively in an orthopteran species within the confines of a sound proof room.

The acoustico-motor response of the female is remarkably fast. At an ambient temperature of about 30 °C the response delay of the female is in the order of 28 ms, as established previously by synthetic sound stimulation of the female (Robinson et al. 1986). It also can be inferred indirectly from the song analysis of duetting pairs by the data shown in Figs. 3 and 4 when subtracting the travelling time of sound through air (ca. 3 ms/m) from the overall latency of the female response for the given distance. The temporal window of the male has a width of up to 35 ms located between about 25 to 55 ms after the start of this call (see Figs. 4 and 5, and Robinson et al. 1986). Thus the onset of the time window is adapted to the net response delay which corresponds to a female sitting in close proximity to him. The outer edge of the male's time window can be converted into a maximum phonotaxis distance. For each increase in communication distance by one metre the overall time delay increases by about 6 ms, so that for an average female (net delay 28 ms) a maximum distance of 4.5 m can be calculated. In fact, a similar value was obtained when analysing the behaviour of duetting pairs (see 4 m in Fig. 4) although the interindividual variation between pairs was remarkable which possibly characterizes different motivational stages.

Figure 3 highlights another important feature of the acoustic behaviour of *Leptophyes*. The female responded to the male over distances of 7 m indicating that she reliably perceived the male sound. However, phonotaxis only occurred up to distances of 3 m. So, although the singing rate of the male (Fig. 3A) and the response timing of the female are consistent over 7 m, for some reason phonotaxis is limited to a smaller distance. Whatever limits phonotaxis has a very sharp cut-off.

Sound intensity and overall latency of the female reply are the most likely limiting factors. Varying these parameters of synthetic female calls independently revealed that in 2/3rd of the individual males tested both intensity and latency were limiting (Fig. 5). In 1/3rd only intensity was the limiting factor.

That intensity should be a limiting factor is intuitively right. Should the sound level of the female response be below the threshold of hearing, the male would not perceive it and so the timing would be irrelevant. In Fig. 2 the difference be-

tween the loudness of male and female sounds is demonstrated. On the average, female sounds are 25 dB less loud than those of males. On the basis that the auditory thresholds of both males and females are the same (about 45–50 dB SPL; Hardt and Rheinlaender, unpublished), it is clear that the females may respond at much further distances than the males can perceive their replies (see Fig. 3). From the examples of Fig. 5 we see that the lowest behavioural hearing thresholds of both males are very close to the previously mentioned neurophysiological thresholds. However, it is noteworthy that a small decrease in sound intensity below the behavioural threshold (1.5 and 2.0 dB in Fig. 5B and A, respectively) leads to the cessation of phonotaxis. It requires that the male's auditory sensitivity should be sharply tuned to small changes in sound intensity which seems to be a fundamental property of insect auditory systems (see also von Helversen 1984; Bailey 1985; Rheinlaender et al. 1986; von Helversen and Rheinlaender 1988).

A further interesting feature of *Leptophyes punctatissima* is its pronounced sensitivity in the time domain. An increase of the female overall response delay by 3 ms beyond a critical value leads to the cessation of phonotaxis (see Figs. 3 and 5A). At present the way in which this time information is processed in the rather 'simple' nervous system of an insect species is completely unknown. In conclusion the heterogeneous data in Fig. 5 suggest that time and intensity are determined independently from each other in the CNS as uncovered in 3 out of 9 cases.

The results obtained in the sound proof room show that for the male the limiting values of time and intensity both coincide with those combinations which constitute the distance characteristic in Fig. 5. It represents the combination of sound intensity and overall latency of a typical female for a given virtual distance to the male. The behavioural processes of the male seem to be adapted to this idealized curve. However, we must consider that in the natural environment there is, normally, a much stronger decrease in sound intensity over distance compared with the 'idealized' conditions of a sound proof room (see e.g. Michelsen and Larsen 1983). Therefore, for the field situation we can expect that in general only the parameter sound intensity should limit the maximum phonotaxis distance. Thus it is possible to speculate that the time window of the male has evolved as a secondary mechanism to isolate related species rather than as a mechanism limiting maximum phonotaxis distance.

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