

SONG RECOGNITION IN FEMALE BUSHCRICKETS *PHANEROPTERA NANA*

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Summary

Unlike most acoustic systems evolved for pair formation, in which only males signal, in many species of phaneropterine bushcrickets both sexes sing, producing a duet. We used the duetting species *Phaneroptera nana* as a model to explore the cues in the male's song that elicit the female's phonoreponse. Different synthetic male songs (chirps containing 2–6 pulses) were presented to *Ph. nana* females, and their acoustic responses were recorded. The threshold of the female response is lowest at 16 kHz (best frequency), coinciding with the dominant frequency of the male song. The specific amplitude pattern of consecutive pulses in the song of the male is not a critical factor in his signal. That is, songs with both a normal and a reversed

order of pulses equally elicit a female response. By systematically deleting pulses from the synthetic male chirp, we found that at least two pulses are needed to elicit a female reply. Under no-choice conditions, increasing the number of pulses did not result in a higher probability of response and did not change the latency of the response; i.e. two pulses are necessary and sufficient to elicit a female response. The range of pulse duration that elicits a female response is 0.2–25 ms, and the inter-pulse silent interval ranges from 5 to 30 ms.

Key words: acoustic duetting, tuning curve, song recognition, communication, bushcricket, *Phaneroptera nana*.

Introduction

Bushcrickets (tettigoniids) use acoustic signalling as a long-distance communication channel for pair formation (for reviews, see Robinson, 1990; Bailey, 1991; Greenfield, 1997). A bi-directional communication system, in which both male and female sing, producing a duet, occurs in several groups of insects, and it is a characteristic of the phaneropterine tettigoniids (Heller, 1990; Spooner, 1995). The chirp of the male is answered, after a short delay, by a short-duration 'click' by the female. To initiate the male's phonotaxis, the female's reply must fall within a defined sensitive time window after the male's call (Robinson et al., 1986; Heller and von Helversen, 1986; Zimmermann et al., 1989; Dobler et al., 1994a). This time window, starting with the termination of each male call, is species-specific (Heller and von Helversen, 1986).

Phaneroptera nana (*Ph. nana nana* sensu Ragge, 1956) is a common bushcricket found on bushes and other vegetation in areas around the Mediterranean. Males emit relatively simple chirps of 1–14 pulses (Fig. 1) dominated by a frequency of 16 kHz (Heller, 1988; E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation). Responsive females will reply to the chirp of the male with a short 'click' approximately 60 ms after the termination of the chirp. Males receiving this female answer will then initiate phonotaxis towards the female (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation).

Previous studies on song recognition in phaneropterine

bushcrickets revealed species-dependent differences. In *Ancistrura nigrovittata*, the female's phonoreponse is activated by a final isolated pulse that characterises the conspecific male's song (Dobler et al., 1994a). In contrast, the female response is not selective in *Poecilimon ornatus* and it is not related to a specific pattern of the male's song (Heller et al., 1997). In the present study, employing synthetic, manipulated songs of males, we used the phonoreponse of *Phaneroptera nana* females to explore the characteristics of the male's call that are important for eliciting a conspecific female response.

Materials and methods

Insects

Phaneroptera nana Fieber females were taken from a laboratory colony established in Jerusalem in 1995. The colony was reinforced several times using insects collected at the same locality (Jerusalem) to avoid inbreeding. The colony was maintained under a 12 h:12 h L:D photoperiod at 30 °C during the photophase and 27 °C during the scotophase. The insects were fed fresh plants (mainly *Plumbago capensis* Tunb.) and flaked oats. Females were transferred immediately after their final moult to a separate room to prevent mating and habituation to the male's song. Bushcrickets were marked and kept individually in separate cages. Virgin females were used in all experiments.

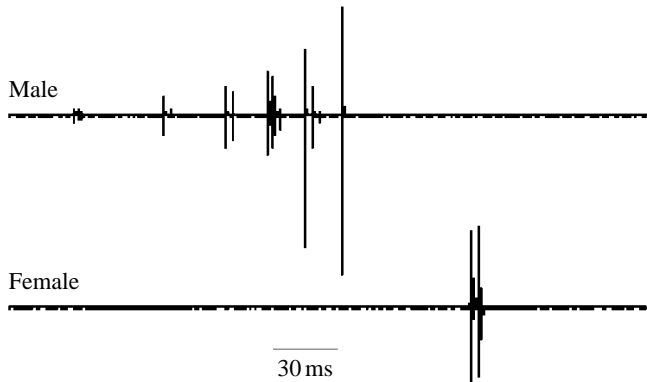


Fig. 1. Oscillograms of a duet of male and female *Phaneroptera nana* recorded at 27 ± 1 °C.

Acoustic stimulation

All experiments were performed in a sound-proof anechoic chamber (60 cm \times 40 cm \times 30 cm). Each female was placed into a vertical cylindrical, wire mesh cage (4 cm diameter, 3 cm height). This cage was placed into the anechoic chamber 15 cm from the loudspeaker (Yuta tweeter horn). The experiments were performed at 27 ± 1 °C under dimmed illumination during the dark phase of the photoperiod. All experiments started after a 15 min 'acclimation' period during which the insect was left undisturbed in the chamber.

The song models were synthesised using Cool Edit software (Syntrilum Software Corporation) installed on a PC. The songs were generated by a 16-bit sound card (Creative Labs, Inc.) and amplified with a Revox amplifier. The output was measured using a Bruel & Kjaer 2203 precision sound level meter and a 1 inch Bruel & Kjaer microphone attached to a Bruel & Kjaer octave filter (model 1613) and displayed on a two-channel oscilloscope (Kenwood). All intensity values are given in dB sound pressure level (SPL; 0 dB = 2×10^{-5} Pa). Because of the relatively slow response of the SPL meter, we

measured playback level by reproducing the sound continuously, measuring function root mean square (RMS) at the position of the female. Both the female response and the stimulus were recorded on separate channels of a four-channel neurocorder (Neuro Data KD-484, up to 44 kS s $^{-1}$). Recordings were later fed to the computer and analysed using Computerscope software (RC Electronics).

To determine the behavioural thresholds at different frequencies, eight song models were generated, each with a different dominant frequency, from 8 to 22 kHz in increments of 2 kHz. The same species-specific temporal pattern (see below), based on mean values for four recorded males, was used for all these model songs. The model songs were presented in a random order, and the female's response was monitored. Songs were presented with decreasing intensity, with a 5 min interval between two consecutive songs. Each song, at a given intensity, was repeated 15 times, one song per second. If no reply was elicited, the song with the lowest intensity that still initiated a response was repeated. If this repeated song was answered, this intensity was assumed to represent the threshold level for that specific frequency. In the two cases in which the female did not reply to a previously answered song, the whole experiment was discarded and the female was replaced.

To determine the role of the amplitude pattern of the pulses, a singing male, interacting with a female, was recorded and one typical song was selected. The song was modified in two ways: (i) the order of the pulses was reversed, and (ii) the amplitudes of all the pulses were equalised. Each of the three model songs (normal, reversed and with equalised pulses) was presented to the same females ($N=5$, 15–20 repetitions per female). The levels of response and response latency (period elapsing between male song onset and female reply) of the females were registered and analysed using the SAS/VMS package (version 6.01).

To analyse the temporal pattern, we used a standard model

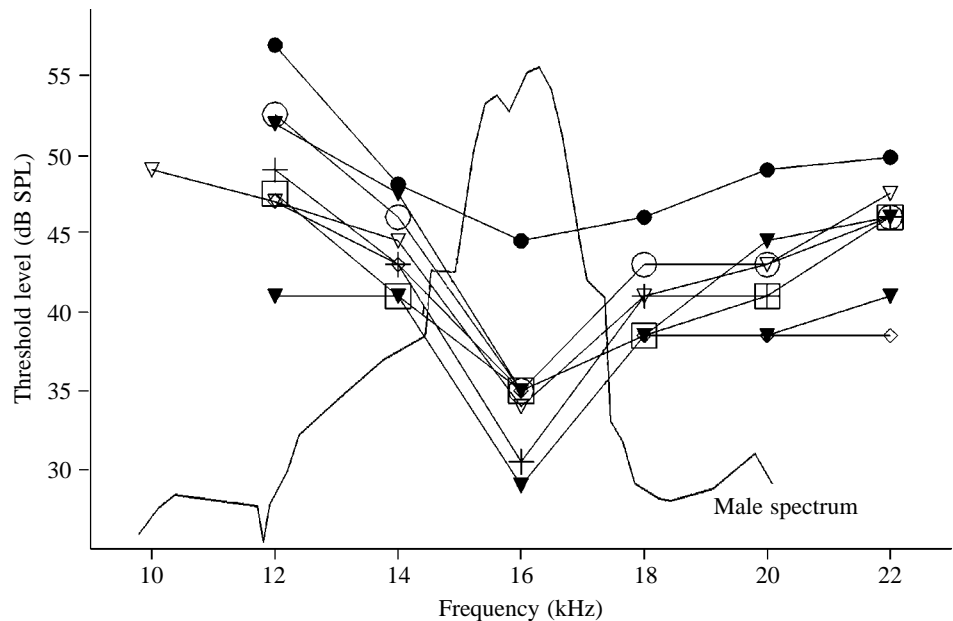


Fig. 2. Frequency discrimination of *Phaneroptera nana* females. The ordinate shows the threshold level of the male model song that still elicited a female response. Behavioural tuning curves for eight females are shown, each indicated with a different symbol. The frequency spectrum of a representative male song (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation) is also shown.

song as a starting point. This model song was constructed using mean values taken from previously recorded males: six uniform, equal-amplitude pulses (pulse duration 0.5 ms), separated by 14 ms gaps, with a 16 kHz dominant frequency. The amplitude of the pulses was 55 dB SPL at the location of the female. This song pattern was changed systematically, each time changing a different song characteristic, until no reply was registered. Periodically, the characteristic species-specific song pattern was presented to ensure that female responsiveness did not decrease. In the case of such a decrease, the female was replaced and the trial was discarded. The levels of response and latencies of the females were registered and analysed as described above.

Results

Frequency sensitivity

The effect of frequency on the behavioural threshold sensitivity (the lowest intensity of male song that elicits a female response) is shown in Fig. 2 for eight females. The responses of *Ph. nana* females show a clear tuning curve. All females consistently showed the greatest sensitivity to a model song at 16 kHz (Fig. 2), which is the dominant frequency of the males' song (Heller, 1988; E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation). Threshold levels for 16 kHz ranged between 29 and 44 dB.

Although inter-individual variability was rather large, all the curves share a similar profile, being asymmetric around the best excitatory frequency. Females are less sensitive to frequencies of 12–14 kHz than to frequencies of 18–20 kHz. This difference exists in each of the females and it is statistically significant ($P=0.016$, Wilcoxon signed-rank test for pairs). An 8 kHz model song did not elicit a response even with a sound level of 70 dB, and only one female replied to the 10 kHz song (Fig. 2). Frequencies higher than 22 kHz were not tested because of technical limitations.

The amplitude pattern of the pulses

As in some other phaneropterines (see Heller and von Helversen, 1986), the final pulses of the song of *Ph. nana* males are much louder than the initial pulses. During the experiments devoted to the study of temporal variables (see below), *Ph. nana* females frequently replied with a fast response before the end of the model song. Since this rarely occurred in interactions with living males recorded in the laboratory (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation), we tested the role of the amplitude pattern in eliciting female reply and its timing.

The females' level of response to a normal song (Fig. 3A) and to a reversed song model (Fig. 3B) was not significantly different (Wilcoxon signed-ranks test, $N=9$, $P>0.5$). However, the response latency (from the onset of the male song model) to the reversed song was markedly shorter; 64.7 ± 11.9 ms compared with that to the normal song (147.3 ± 29.7 ms; means \pm S.D., $N=60$).

Despite these results, the high-intensity final pulses in the

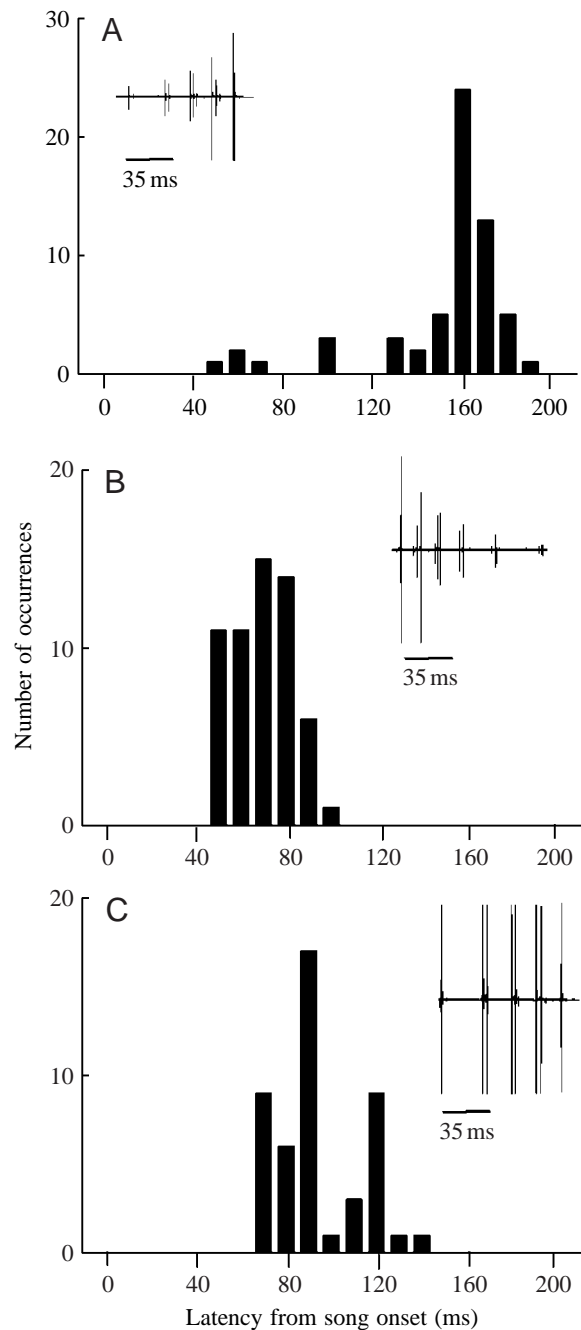


Fig. 3. The effect of the amplitude pattern of the male song on the female phonoreponse in *Phaneroptera nana*. The distributions of the latencies of the response (from the onset of the male song) are given for five females, 15–20 samples per female. The same females were tested with (A) natural song, (B) reversed song and (C) model song with pulses of equal amplitude (see insets).

normal song do not seem to encode the termination of the song; this is shown by the female response to the model song containing pulses of uniform amplitude, in which the pulses were ordered as in the original song (Fig. 3C). This model song was as effective as a normal song in activating a female response (Wilcoxon signed-ranks test, $N=9$, $P>0.5$), but the

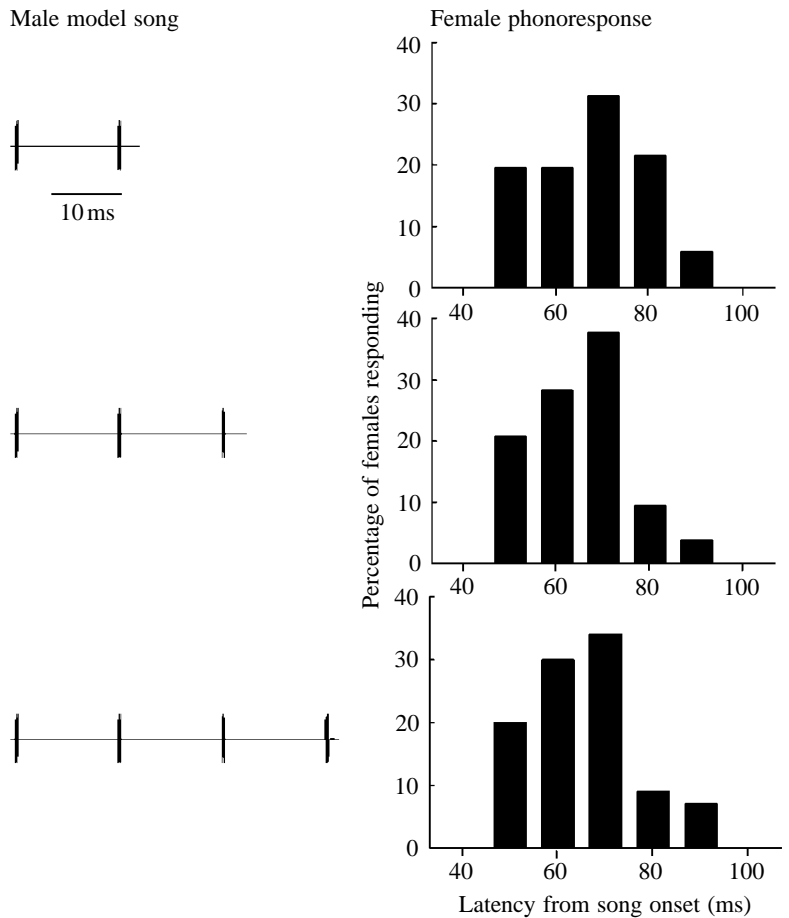


Fig. 4. Latencies of the *Phaneroptera nana* female phonoresponse (right) from the onset of male model songs containing varying numbers of pulses (left). All songs had a 0.5 ms pulse duration and a 14 ms interval(s) between pulses, which are the mean values taken from songs recorded from four males. Latencies are given for four females, 15 samples per female. The ordinate shows the distribution (as a percentage) of responses for the given latencies.

latency of the response was again shorter than for normal song, 88.5 ± 19.5 ms ($N=47$). The latencies of the responses to the three song models were all significantly different ($P < 0.0001$, one-way analysis of variance, ANOVA, Bonferroni *post-hoc* comparisons). The latencies for the model song with pulses of uniform amplitude (Fig. 3C) were slightly longer than those for the reversed song (Fig. 3B), presumably because, in this stimulus, the interval between the first two pulses was greater (29 ms *versus* 14 ms in the reversed song, compare insets in Fig. 3B,C).

These results indicate that the amplitude pattern of the song does not determine the timing of the female response. The female response is probably activated only by the first two pulses (see below) when they occur above some specific threshold intensity. In a normal song (Fig. 3A inset), the first few pulses are presumably too low in intensity to elicit a response, and the female response therefore rarely occurs before the termination of the song.

Temporal pattern

Presentation of synthetic model songs (with pulses of uniform amplitude) containing 2–6 pulses did not produce a change in the level of female responses. The minimum number of pulses necessary to elicit a female response was two, and a two-pulse song model was no less effective than longer songs. Fig. 4 shows the distribution of the latencies of the females'

responses (measured from the onset of the male's song) to synthetic male songs containing different numbers of pulses. There was no significant difference between the latencies of responses to two-, three- and four-pulse songs (ANOVA, $F_{2,76}=0.642$, $P=0.53$; Kolmogorov–Smirnov test for normality, $P > 0.1$). Thus, pulses that are emitted after the first two pulses are apparently not effective in eliciting a female response; two pulses are both sufficient and necessary to activate a female response.

The range of intervals between two pulses that elicited a female response was 5–30 ms; females reacted best to models with intervals of 15–25 ms (Fig. 5A). The timing of the female response was highly correlated with the inter-pulse interval (Fig. 5B), indicating that the female response is being triggered by the second pulse ($r^2=0.78$, $F_{1,8}=28.49$, $P < 0.001$). The latencies of the female's response from the second pulse were rather constant, and the slope of the regression line (Fig. 5B) was not significantly different from zero ($r^2=0.30$, $F_{1,8}=3.50$, $P > 0.09$). Latencies from the second pulse averaged 45.5 ± 6.9 ms (mean \pm s.d., $N=3$ females, 20 samples each).

The optimal pulse duration ranged between 0.3 and 15 ms, although pulses with a duration of 0.2 ms, as well as with durations of 20 and 25 ms, were occasionally also answered; pulses of 32 ms did not elicit a response (Fig. 6). This is a remarkably wide range compared with the natural pulse

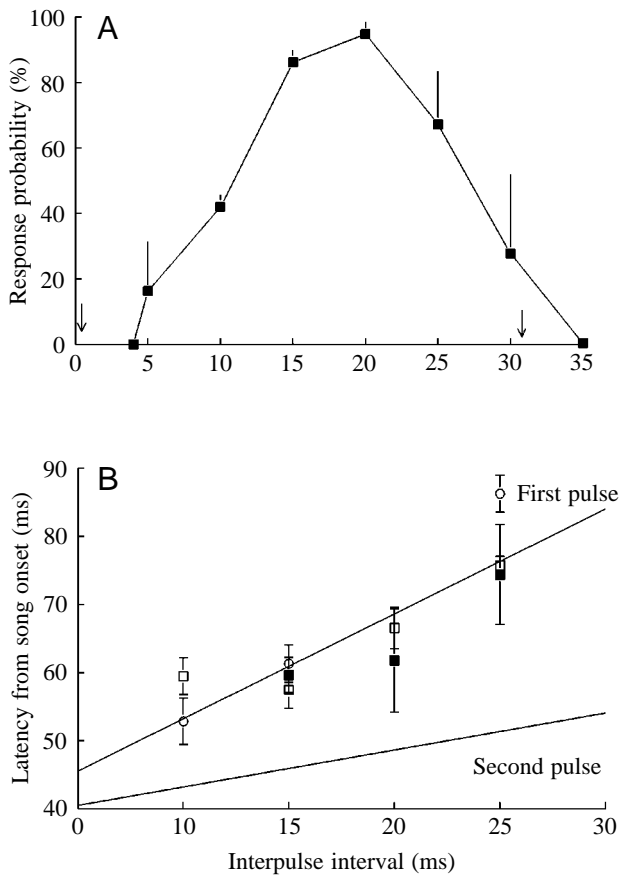


Fig. 5. Effects of the inter-pulse interval of a two-pulse model song on the female phonoresponse in *Phaneroptera nana*. (A) Mean response probability and standard deviation for nine females for different inter-pulse intervals. Arrows indicate the natural range of inter-pulse interval in the male's song. (B) The effect of increasing the inter-pulse interval on the latency of the female response from song onset (mean and standard deviations) are given for three females, 20 samples each. Each symbol represents a different individual. The regression line for latencies from song onset ($r^2=0.78$, $F_{1,8}=28.49$, $P<0.001$) and for latencies from the second pulse terminating the song ($r^2=0.30$, $F_{1,8}=3.50$, $P>0.09$) are shown. The data points for the regression line for the second pulse (lower line) are the same as for the upper line minus the respective inter-pulse interval.

duration, which is in the range 0.1–0.7 ms (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation).

Discussion

Like other phaneropterine females, *Ph. nana* females respond with a short latency and a defined acoustic signal to the song of a conspecific male. This phonoresponse of the females offers an excellent model system in which to study recognition processes (Dobler et al., 1994a,b; Heller et al., 1997).

Ph. nana females show a clear spectral tuning of their phonoresponse (Fig. 2), and this spectral sensitivity is well

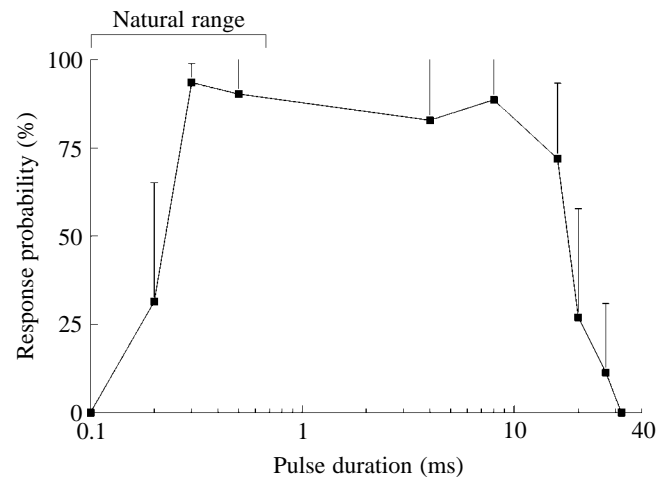


Fig. 6. Effect of pulse duration in the male model song on the female phonoresponse in *Phaneroptera nana*. Mean response probability and standard deviation of nine females, $N=69$ –228 samples per data point are given. The stimulus consisted of two pulses with a 14 ms interval. The natural range of pulse duration in the male's song is also shown.

matched to the male song spectrum. Such matching has also been reported in other orthopterans (Hill and Boyan, 1977; Hill and Oldfield, 1981; Lin et al., 1993; Dobler et al., 1994b) and has recently received attention as a possible cue for species discrimination (Meyer and Elsner, 1996, 1997). As in *Ph. nana*, the song of *Ancistrura nigrovittata* males peaks at 15–16 kHz, and in this species auditory threshold data are available in addition to behavioural tuning curves (Dobler et al., 1994b). The threshold at the sensitivity peak of behaviour (i.e. approximately 16 kHz) is remarkably close to the lowest threshold of the auditory organ. The complete hearing range, however, is much broader than the behaviourally effective range.

As in some other phaneropterines (Heller and von Helversen, 1986), the song of *Ph. nana* males has a characteristic 'triangular' amplitude pattern, with the amplitude of the pulses increasing towards the end of the song (Fig. 1). Females frequently replied to the model song before its termination, a behaviour that rarely occurs in duets with living males recorded in the laboratory (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation). We tested, therefore, whether the amplitude pattern of the pulses indicates the end of the song for the female. The results show that a model song in which the order of the pulses in the natural song was reversed elicited responses with significantly shorter latencies (Fig. 3B). However, this effect seems to be merely a result of the high amplitude of the early pulses in the reversed song (originally the final pulses of the normal song), as demonstrated by the female's response to a model song with pulses of uniform amplitude (Fig. 3C). The increase of the amplitude of the first pulses of the normal song caused shorter latencies. These results suggest that the initial pulses in the normal song are too low in intensity to be detected.

Alternatively, these initial pulses may be disregarded by the female because the low intensity may indicate that the male is relatively far away. In either case, the female response is activated towards the end of the natural song of the male. Conversely, the results suggest that the distance between the male and the female will have a significant effect on the timing of the female response. Latency will decrease with shorter range because of the shorter time taken for the song to travel and the intensity/latency correlation (Zimmermann et al., 1989); if the male and the female are relatively close, she will be more likely to respond to the early pulses of the male's song.

There is a difference between males and females with respect to the time reference for the female response; in another study, we used the latency from the termination of the chirp (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation) because this interval dictates whether the response falls within the male's putative sensitive time window. However, the female response is initiated by the first detectable pulses of the chirp.

An important finding of this study is that the code that is sufficient to activate the female's response is based on two pulses, each of 0.2–25 ms in duration, separated by a gap of 5–30 ms. This simple pattern releases a short-latency response by the female; the resulting simple duet is presumably sufficient to allow male phonotaxis.

A two-element song has also been described in another phaneropterine bushcricket, *Ancistrura nigrovittata* (Dobler et al., 1994a). However, in this bushcricket, the first element consists of a group of 5–9 syllables which, after an interval of approximately 400 ms, is followed by a second element consisting of one final syllable. It was shown that the female response depends on the recognition of the syllable group and that the perception of the final syllable serves as a trigger. The situation in *Ph. nana* may represent a primitive state that gave rise to more elaborate signals; a comparative study of phaneropterine songs (Heller, 1990) indicated that the primitive song consisted of single syllables that were loosely arranged, separated by distinct intervals and gradually increased in amplitude. Thus, the simple song of *Ph. nana* males may be considered primitive, and *Ph. nana* females may demonstrate an elementary pattern recognition system.

Ph. nana females disregard inter-pulse intervals shorter than 5 ms (Fig. 5). This type of 'tolerance' of short inter-pulse intervals was also observed in the bushcricket *Ancistrura nigrovittata* (Dobler et al., 1994a). In the song of *Ph. nana* males, the interval between consecutive pulses is highly variable (Fig. 5A) (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation), with some pulses following each other closely (see Fig. 1). Successive pulses separated by intervals shorter than 5 ms will be interpreted by the female as one long pulse. If longer pulses are more attractive, males may extend the functional range of the pulse duration by producing many closely spaced pulses. It is noteworthy that the natural song of *Ph. nana* males consists of as many as 15 pulses, often separated by less than 5 ms (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in

preparation; Fig. 1). The range of pulse duration that females accept is markedly longer than the natural range (Fig. 6); thus, males may exploit female receptivity by producing bursts of closely spaced pulses.

In another study on *Ph. nana* (E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener, in preparation), we found that females, when interacting with two singing males (two-choice design), preferred to respond to males that produced a greater number of pulses in their songs. The discrepancy between this finding and the present results may be accounted for by the differences between no-choice and two-choice experimental designs (e.g. Doherty, 1985). E. Tauber, D. Cohen, M. D. Greenfield and M. P. Pener (in preparation) also tested *Ph. nana* females interacting with one male (a no-choice design) and found no significant female preference; the proportion of female replies to different males did not differ significantly. The procedure employed in the present study is basically a no-choice design.

Recently, an indiscriminate behaviour was demonstrated in females of the phaneropterine *Poecilimon ornatus* (Heller et al., 1997). *P. ornatus* females respond to all types of acoustic signals tested if they are at least 1–3 ms in duration and have a sound pressure level of 70 dB or greater. Here, we report that the response behaviour of *Ph. nana* females is discriminative; such simple pattern recognition may prevent heterospecific pairing. This is apparently the result of the bi-directional communication system of phaneropterine bushcrickets: conspecific pairing is achieved because both the male and the female must recognize each other's signal.

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