Recognition of calls with exceptionally fast pulse rates: female phonotaxis in the genus *Neoconocephalus* (Orthoptera: Tettigoniidae)

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Summary

Male *Neoconocephalus robustus* and *Neoconocephalus bivocatus* produce remarkably fast calls, with pulse rates of approximately175–200 Hz. The temporal call patterns differ significantly between the two species. Male *N. robustus* produce calls with a single pulse rate of 200 Hz. In *N. bivocatus*, pulses are repeated with alternating periods, resulting in distinct pulse pairs: approximately 175 pulses s^{-1} are grouped into 87 pulse pairs s^{-1}. In order to identify the temporal parameters used to recognize calls with such fast pulse rates, female call recognition in both species was tested during phonotaxis on a walking compensator. Female *N. robustus* were attracted to calls without amplitude modulation. Amplitude-modulated signals were equally attractive, as long as the silent intervals were short enough. The maximally tolerated interval duration varied with pulse duration. Female *N. bivocatus* did not require the paired-pulse pattern but were attracted to call models in which each pulse pair was merged into one long pulse. Females used the pulse rate to recognize such signals: pulse rates close to 87 Hz were attractive, largely independent of the duty cycle. Thus, females of the sibling species *N. robustus* and *N. bivocatus* used qualitatively different call recognition mechanisms.

Key words: acoustic communication, temporal pattern recognition, hearing, amplitude modulation, phonotaxis, *Neoconocephalus*.

Introduction

The communication signals of insects and anurans often contain highly repetitive elements, which are either monotonously repeated or grouped into higher order patterns (reviewed in Ewing, 1989; Gerhardt and Huber, 2002). The temporal pattern of these signals is often used by the receiver side of the communication system for call recognition. Several behavioral studies have identified the temporal characteristics used for this task. Specific temporal parameters that have been identified as important for call recognition include: (1) the rate (or period) of sound pulses (e.g. Hennig and Weber, 1997; Plewka, 1993; Thorson et al., 1982), (2) the duty cycle of the signal (e.g. Helversen and Helversen, 1983; Schul, 1998) or (3) absolute durations of sound pulses and/or the intervals between pulses (e.g. Helversen, 1972; Hennig, 2003; Schul and Bush, 2002), or combinations of such parameters (e.g. Doherty, 1985).

The pulse repetition rates of male calling songs of insects and anurans are predominantly in the range of 10 Hz to 60–80 Hz (e.g. Heller, 1988; for a notable exception, see Heller, 1986). Accordingly, durations of pulses and intervals are typically 6 ms or longer. The auditory pathways of most insects and anurans are well able to encode temporal parameters of such rates and durations (reviewed in Gerhardt and Huber, 2002).

Male calls in the Tettigoniid genus *Neoconocephalus* are unusually fast. Pulse rates in the range of 200–250 pulses s^{-1} are common in this genus: 21 out of 25 species with described calls have pulse rates well above 100 Hz (Greenfield, 1990). It is questionable whether the sensory system is able to faithfully encode the temporal pattern of such fast calls: the temporal acuity of insect auditory receptor cells has been found to decrease for amplitude modulation rates above 100 Hz (e.g. Prinz and Ronacher, 2002; Surlykke at al., 1988). Additionally, the ascending auditory pathway will likely limit transmission to even lower modulation rates (e.g. Schildberger, 1984). Nevertheless, fine-scale temporal patterns of the calls vary distinctly among *Neoconocephalus* species (Greenfield, 1990), especially between sibling species with overlapping ranges of occurrence. For example, the sibling species *N. robustus* and *N. bivocatus* have wide, overlapping ranges in eastern North America. The temporal patterns of their calls differ distinctively (Walker et al., 1973; Büttner, 2002). The calls of *N. robustus* consist of pulses monotonously repeated at a rate of 200 pulses s^{-1} (at 25°C; Fig. 1A). In *N. bivocatus*, pulses are repeated with alternating periods, resulting in distinct pulse pairs (Fig. 1A). The repetition rate of these pulse pairs is 87 Hz (at 25°C), i.e. ~175 individual pulses s^{-1} (Büttner, 2002). This strongly suggests that the temporal patterns are actually used for call recognition, despite their fast pulse rates.

Here, we study the selective phonotaxis in females of two closely related species, *N. robustus* and *N. bivocatus*. We focus
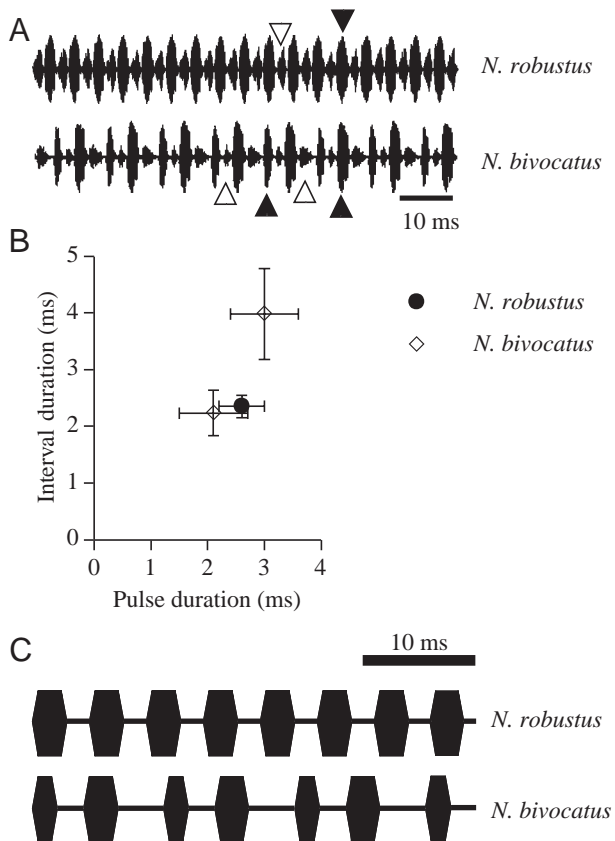
Fig. 1. (A) Oscillograms of calls recorded from male *N. robustus* (top trace) and *N. bivocatus* (bottom trace) at 25°C. The filled arrowheads indicate sound produced during closing movements; open arrowheads represent the sound generated during the opening movements of the tegmina. (B) Durations of the pulses produced during the closing movements of the wings and of the intervals between them (Walker, 1975) in the calls of *N. robustus* and *N. bivocatus* (mean ± s.d.; *N*=12 and 8, respectively). Due to the two alternating pulse periods of *N. bivocatus*, two combinations of pulse and interval are given for this species; pulse durations were combined with the duration of the following interval. (C) Oscillograms of the models of the conspecific calls of *N. robustus* (top trace) and *N. bivocatus* (bottom trace) used in this study. Note the different time scales in A and C.

on female selectivity for temporal call patterns to learn whether the fast temporal patterns of their calls contain useful information for call recognition and, if so, to identify the temporal call parameters actually used for call recognition, i.e. the recognition mechanism used by the females. Identifying such behavioral recognition mechanisms, which classical ethology called 'innate releasing mechanisms' (Lorenz, 1943; Tinbergen, 1953), is a prerequisite for the understanding of the neuronal basis of call recognition.

Materials and methods

Animals

We collected female *Neoconocephalus robustus* and *N.* *bivocatus* from the field as nymphs in Boone County, MO, USA and identified them after Froeschner (1954) and Walker et al. (1973). The insects were kept at 20–25°C and a 14 h:10 h light:dark cycle. The females were kept for at least two weeks after their adult molt before they were used in experiments. Females were tested for up to five weeks, during which we detected no changes in their selectivity.

Phonotaxis experiments

We conducted behavioral tests on a walking compensator (Kramer treadmill; Weber et al., 1981) in an anechoic chamber at 25±1°C. Briefly, the insects were placed on top of a sphere, free to walk but kept in place by compensatory sphere rotations, while acoustic signals were presented from loudspeakers located in the insect's horizontal plane. The intended direction and speed of the animal were read out from the control circuitry. The experiments were performed in the dark except for an infrared light used to monitor the movements of the animal on the sphere. For details, see Weber et al. (1981) and Schul (1998).

Stimulation

We generated synthetic signals using a custom-developed DA-converter/amplifier system (16-bit resolution, 250 kHz sampling rate). The signals were delivered *via* one of two loudspeakers (EAS 10TH400C or Motorola KSN1218C) mounted at a distance of 150 cm in the horizontal plane of the insect and separated by an angle of 115°. We adjusted signal amplitude to 80±1 dB peak SPL (re. 2×10^{-5} Pa) using a 1/4″ condenser microphone (G.R.A.S. 40BF), positioned 1 cm above the top of the sphere, and a Bruel and Kjaer sound level meter (B&K 2231). This amplitude is representative for a distance of 2–3 m from a calling male (Büttner, 2002; Schul and Patterson, 2003).

The calls of *N. robustus* and *N. bivocatus* have similar spectral composition (Schul and Patterson, 2003). Highest amplitudes are present in a narrow low-frequency band, and the frequency components at ultrasonic frequencies are at least 20 dB softer than the low-frequency band. The center frequency of the low-frequency band differs significantly between the two species (*N. robustus*, 7 kHz; *N. bivocatus*, 10 kHz). We used pure tones of 7 kHz (for *N. robustus*) or 10 kHz (*N. bivocatus*) as carrier signals, to which we subsequently applied amplitude modulations. This simplification of the spectral call structure did not noticeably influence the attractiveness of the stimuli (see below).

The temporal patterns used as models of the natural calls were based on population mean values determined by Büttner (2002) at 25°C (Fig. 1B). The call model for *N. robustus* consisted of a continuous train of pulses of 3 ms duration, separated by silent intervals of 2 ms duration, resulting in a pulse rate of 200 Hz (Fig. 1C). The call model for *N. bivocatus* consisted of a continuously repeated train of paired pulses, each consisting of two pulses of 2.2 ms and 3.0 ms duration with an interval of 2.3 ms in between. These paired

pulses were repeated after an interval of 4.0 ms, resulting in a paired-pulse rate of 87 Hz (Fig. 1C). These call models were used as control stimuli throughout this study. For both species, female responses to these call models did not differ significantly in walking speed or quality of orientation (= vector length) from responses to high-quality recordings of conspecific calls.

In the first experiment, we tested the attractiveness of a continuous sine wave without amplitude modulation. In all other experiments, we varied pulse duration and interval duration independently. All stimuli were presented as continuous signals without a second-order time pattern modulating the pulse pattern.

Experimental protocol

The experimental protocol is described in detail in Schul (1998) and Bush et al. (2002). All stimuli were presented twice for approximately 1.5 min, with loudspeakers switched between the two presentations. At the beginning of each series, the control stimulus was presented, followed by two or three test stimuli, then another control, etc. Between stimuli, a 1-min period of silence was imposed. Each experimental series lasted between 30 and 60 min, during which up to nine experimental stimuli (plus four controls) were presented. We varied the sequence of stimulus presentation among the individual females tested.

Data analysis

To evaluate the relative response of a female during a test situation, we calculated a phonotaxis score (PS; Schul, 1998), which included measures for three criteria that positive phonotaxis should meet: (1) the relative walking speed, describing the locomotion activity elicited; (2) the vector length, describing the accuracy of orientation and (3) the orientation relative to the orientation during the control stimulus. Phonotaxis scores range from approximately +1 (perfect positive phonotaxis) to –1 (perfect negative phonotaxis). Phonotaxis scores close to 0 indicate either no response or random orientation (for details of the data analysis and calculation of the phonotaxis score, see Schul, 1998). Phonotaxis score for the control stimulus ranged between 0.8 and 0.95 for most females of both species.

We present all data as means ± S.E.M. Female responses were considered significant if two criteria were met: (1) the mean phonotaxis score was significantly greater (Mann–Whitney *U*-test, *P*<0.05; Zar, 1984) than a hypothetical population of responses of zero with identical sample size and (2) the average response was at least 50% of the response to the model of the conspecific call. Since the second criterion was always much more stringent than the first, we do not present the results of the *U*-tests in the text. Note that the application of a significance criterion merely emphasizes the shape of the response fields in order to clarify the mechanism used for call recognition and was not meant to classify stimuli as 'recognized' and 'not recognized' (for a detailed discussion, see Bush et al., 2002).

Results

The first experiment was conducted to determine whether female *N. robustus* and *N. bivocatus* require the pulsed structure of their conspecific calls for call recognition (Fig. 2). We tested the attractiveness of an unmodulated signal (i.e. a continuous sine wave) relative to that of the call models. In *N. robustus*, the mean phonotaxis scores in response to the unmodulated sine wave (0.95±0.04, *N*=9) and in response to the conspecific call model (0.91±0.04, *N*=9) were comparable (Mann–Whitney *U*-test, *U*=45, *N*=*M*=9, *P*=0.69, N.S.). Thus, in *N. robustus*, the unmodulated signal was as attractive as the conspecific call model.

Female *N. bivocatus* responded to the model of their conspecific call with a phonotaxis score of 0.88±0.03 (*N*=9). However, the unmodulated signal did not elicit significant responses in this species (Fig. 2B); the mean phonotaxis score in response to this stimulus (0.23±0.10, *N*=9) was significantly lower than that in response to the conspecific call (Mann–Whitney *U*-test, *U*=81, *N*=*M*=9, *P*<0.05). Thus, female *N. bivocatus* require some temporal pattern for call recognition, while in *N. robustus* amplitude modulation is not required.

Experiments with N. robustus

Experiment 1 (Fig. 2) demonstrated that female *N. robustus* responded to an unmodulated signal as well as to their call model. In the next experimental series, we tested which amplitude modulations were attractive for this species by independently varying pulse duration and interval duration. We tested a total of 24 such combinations. The results of this experiment are given in Fig. 3.

Female *N. robustus* responded with high phonotaxis scores (between 0.87 and 0.96, *N*=8 each) to signals with intervals of 2 ms or less, independent of pulse duration. With increasing interval duration, the signal became less attractive regardless
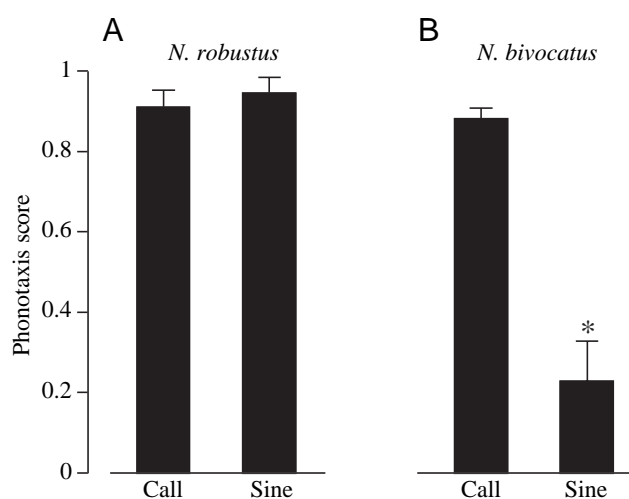
Fig. 2. Phonotaxis score (mean ± S.E.M.; *N*=9 each) of female *N. robustus* (A) and *N. bivocatus* (B) in response to the model of the conspecific call (left bar) and to an unmodulated sine wave (right bar). Asterisk indicates a significant difference from the corresponding conspecific call model (*P*<0.05, Mann–Whitney *U*-test).
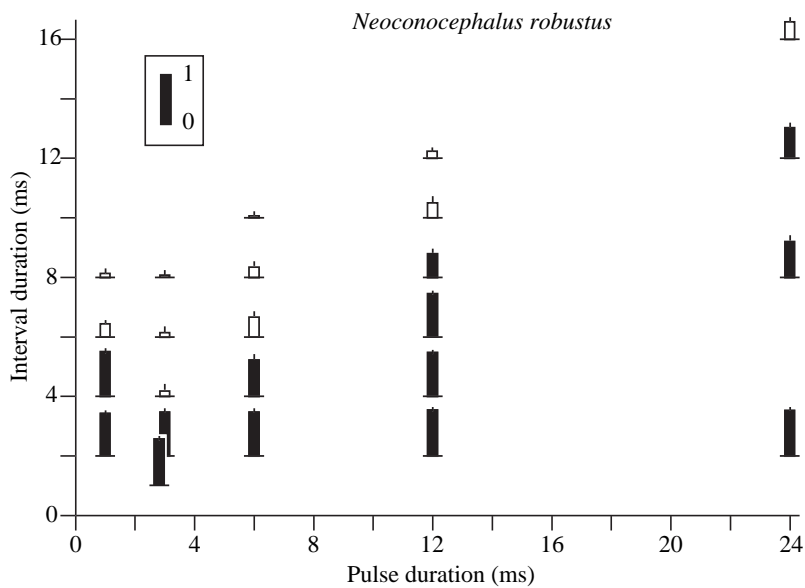
Fig. 3. Importance of pulse duration and interval duration for phonotactic responses of *N. robustus*. The bars indicate the phonotaxis score (mean ± S.E.M.; *N*=8–9) for the respective parameter combination (see inset for the scale of the phonotaxis score). The baseline of each bar is positioned on the interval duration. Filled bars indicate significant responses, and white bars indicate non-significant responses.

of pulse duration (Fig. 3). At the pulse duration of the call model (3 ms) an interval duration of 4 ms resulted in a mean phonotaxis score of 0.13±0.11 (*N*=8). For longer pulses, female responses did not decline for such short intervals; as pulse length increased, the maximum interval duration that still elicited significant responses also increased. At a pulse duration of 1 ms, females responded strongly to interval durations of 2 and 4 ms; intervals of 6 and 8 ms did not elicit significant female responses (Fig. 3).

Experiments with N. bivocatus

The first experiment (Fig. 2) demonstrated that an amplitude-modulated signal was required for significant phonotaxis of female *N. bivocatus*. We designed the next experimental series to determine the simplest temporal pattern that would elicit significant phonotaxis. The model of the conspecific call served as control, while the pulse and interval durations occurring in the double pulse pattern of this signal (Figs 1C, 4B, top trace) were tested in various combinations (Fig. 4).

Three test stimuli used the duration of the first (= shorter) pulse of the double pulse (2.2 ms) in combination with three interval durations (Fig. 4, tests 1–3): (1) 2.3 ms, the interval within each double pulse; (2) 4.0 ms, the interval between double pulses and (3) 9.3 ms, an interval duration resulting in a pulse rate equivalent to the double pulse rate of the call model. None of these stimuli elicited significant responses (Fig. 4).

Next, we tested three stimuli based on the duration of the second (= longer) pulse of the double pulse (3 ms), using interval durations corresponding to those used for tests 1–3: the interval durations used were 2.3 ms, 4.0 ms and 8.5 ms (Fig. 4, tests 4–6). Again, none of these three stimuli elicited significant responses from female *N. bivocatus*.

For the last two stimuli, we substituted the double pulse of

the call model with one longer pulse. One of the stimuli (Fig. 4, test 7) had a pulse duration of 5.2 ms, i.e. the duration of both pulses added (2.2+3.0 ms); the other stimulus (test 8) had a pulse duration of 7.5 ms, which was the duration of a double pulse including the silent interval (2.2+2.3+3.0 ms). Both of these temporal patterns elicited responses as strong as the control stimulus [phonotaxis scores of 0.88±0.03 (test 7), 0.86±0.02 (test 8) and 0.92±0.04 (control), *N*=8].

This experiment demonstrated that the more elaborate temporal structure of the natural call, with two alternating pulse periods, was not necessary to elicit phonotaxis in *N. bivocatus*. Rather, females responded to a pulse with the duration of the natural call's double pulse, repeated at the normal rate. This finding leads to the question of which combinations of pulse duration and interval duration are attractive for the females.

We designed the last set of experiments to determine the effective range of pulse durations (equivalent to a merged double pulse) and interval durations (equivalent to the interval between double pulses). We varied the duration of both parameters independently and tested a total of 50 combinations. The results of this experiment are given in Fig. 5.

Female *N. bivocatus* showed significant phonotaxis to stimuli when the pulse period (i.e. the sum of pulse duration and interval duration) was close to 11.5 ms, which is the equivalent of a pulse rate of 87 pulses s⁻¹. This corresponds to the rate of double pulses in the male calls of this species. Such responses are located in the response field (Fig. 5) along a diagonal from top left to bottom right. Response magnitudes decreased sharply to both higher and lower pulse rates.

The attractiveness of stimuli with pulse rates close to 87 pulses s⁻¹ was largely independent of the pulse duration: only for pulses of ≤3 ms did responses decline sharply. At the other end of the attractive field, an interval duration of 1 ms
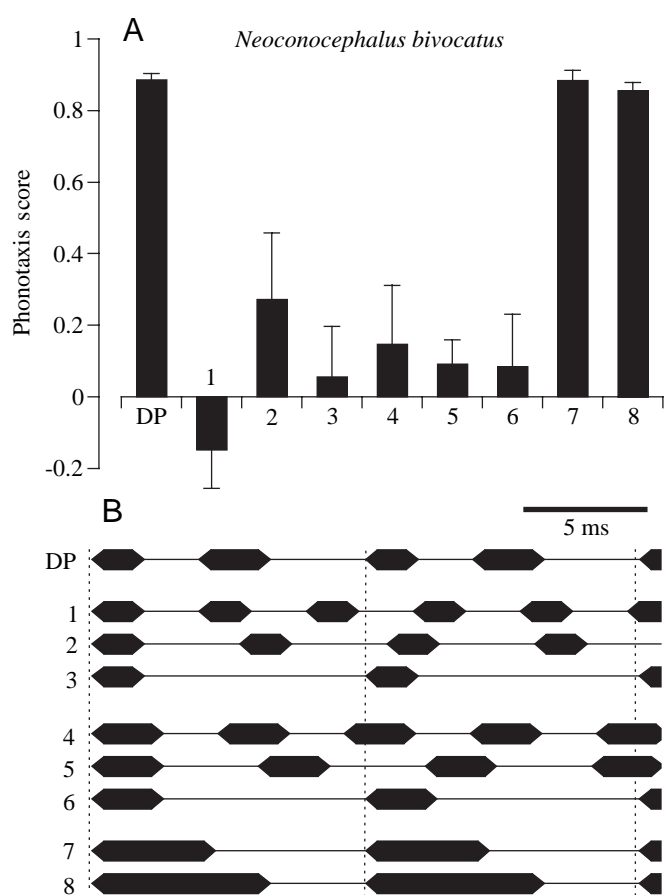
Fig. 4. (A) Phonotaxis scores (mean ± s.e.m.; *N*=8) of female *N. bivocatus* to different stimuli. (B) Oscillograms of the stimuli used in A. These stimuli test the importance of the temporal parameters occurring in the pattern of the conspecific call. DP indicates the model of the conspecific call. For further description of the stimuli, see text.

was sufficient to maintain high phonotaxis scores (pulse 10 ms/interval 1 ms, PS=0.83±0.06).

Only one stimulus outside of the above-described response field elicited significant responses (pulse 4.5 ms/interval 1 ms, PS=0.55±0.1). This stimulus had a pulse rate of 182 Hz, which is about twice the pulse rate of the other attractive stimuli. Stimuli with half the pulse rate (43 Hz) were not attractive (pulse 15 ms/interval 8 ms, PS=–0.01±0.12; 7.5 ms/15.5 ms, PS=0.09±0.16).

Discussion

Our results demonstrated that both *N. robustus* and *N. bivocatus* were highly selective for temporal call patterns (see below). However, the underlying recognition mechanisms were strikingly different. Female *N. robustus* responded to signals without amplitude modulation; at pulse durations typical for this species, interruptions of a few ms within a stimulus rendered the call unattractive. By contrast, female *N. bivocatus* required a distinct amplitude modulation for call

recognition: females responded to calls containing a pulse rate of 87 Hz.

At this point, we want to emphasize that, although *N. robustus* females responded to a signal without amplitude modulation, this does not mean that they are unselective for temporal pattern. Rather, such unmodulated signals have a highly specific pattern, and the mechanism to recognize it may be as specific or selective as a mechanism that detects specific amplitude modulations (e.g. a particular pulse rate). In light of our results, the common interpretation that responses to unmodulated noise represent responses to 'random signals' and indicate unselectivity (e.g. Morris and Fullard, 1983; Ryan and Rand, 1995) should be revisited; females might be highly selective and recognize the temporal pattern of 'no amplitude modulation'.

N. robustus

Female *N. robustus* responded to a continuous, unmodulated sine wave as well as to the model of the conspecific call. Amplitude-modulated signals (such as the call model) were attractive, as long as the intervals were short (Fig. 3). The maximum interval duration tolerated by the females increased as pulse durations became either longer or shorter than that of the call model (3 ms). When pulses are longer, fewer intervals appear in the signal per unit time. An interval of a given duration will, over time, therefore have a smaller negative effect at long pulse durations than at shorter pulse durations. A different process is probably responsible for the increase in tolerated interval duration when pulse duration is only 1 ms. The sensory system probably cannot faithfully encode pulse durations in the range from 1 to 3 ms (Rössler and Schul, 1993). Accordingly, female responses at pulse durations of 3 ms and 1 ms decline once the sum of pulse and interval duration (i.e. the pulse period) surpasses 5 ms (see Fig. 3).

Females of three other katydid species were reported to recognize signals without amplitude modulation; *Conocephalus nigropleurum* (Morris and Fullard, 1983), *C. brevipennis* (Guerra and Morris, 2002) and *Tettigonia caudata* (Schul, 1998) respond to continuous noise stimuli. Because male calls in *T. caudata* have a significantly longer duty cycle than the calls of congeners, the call recognition mechanism of this species was interpreted as filtering a minimum duty cycle – the unmodulated signal has 100% duty cycle and thus is attractive. However, duty cycle recognition does not adequately explain the data from *N. robustus*; a phonotaxis score of 0.5 occurred both when pulses and intervals were of equal duration (3 ms) and when the pulses (24 ms) had twice the duration of the intervals (12 ms).

Although female call recognition requires an unmodulated signal, male *N. robustus* produce a pulsed call with a pulse rate of 200 pulses s^{-1}. The call production mechanism prohibits unmodulated calls, but the fast pulse rate ensures that the call is recognized as unmodulated by the females. Another feature of the *N. robustus* call supports this interpretation; the pulses produced during the opening movement of the wings are significantly louder than in four other species of
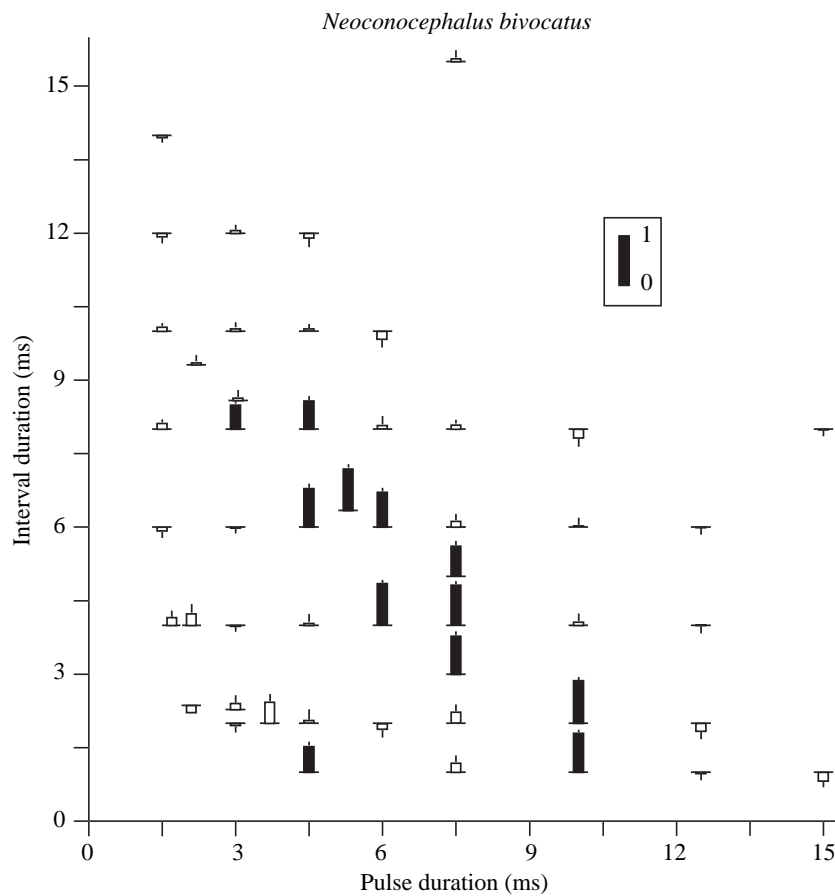
Fig. 5. Importance of pulse duration and interval duration for phonotactic responses of *N. bivocatus*. The bars indicate the phonotaxis score (mean ± S.E.M.; *N*=8–10) for the respective parameter combination (see inset for the scale of the phonotaxis score). The baseline of each bar is positioned on the interval duration. Filled bars indicate significant responses, and white bars indicate non-significant responses.

Neoconocephalus: in *N. robustus*, their mean amplitude is 75% of the closing pulses, while in the other species their amplitude is between 20 and 40% (Büttner, 2002). These large opening pulses break up the interval between the closing pulses so that, effectively, only gaps of 1 ms occur in the males' signals. This ensures that male calls are still recognized, even if the pulse rate is considerably lower, e.g. a call from a male at lower temperature.

N. bivocatus

In contrast to *N. robustus*, female *N. bivocatus* require a distinct amplitude modulation: they are attracted only to calls containing a pulse rate of 87 pulses s⁻¹. Additionally, pulses have to be longer than 3 ms. Male calls contain approximately 175 pulses s⁻¹ but, by grouping the pulses into pairs, they introduce the required 87 Hz component. Females ignore the interval within the pulse pair (2.3 ms duration), effectively merging the two pulses (2.2 and 3.0 ms duration) into one long pulse of sufficient duration for call recognition to occur. The duration of the interval ignored by *N. bivocatus* females is similar to the duration of the interval accepted by *N. robustus* females in 'unmodulated' signals.

Schul (1998) described a call recognition mechanism in *Tettigonia viridissima* that is similar to the one we describe in *N. bivocatus*. In *T. viridissima*, males produce a double pulse pattern, and female call recognition merges the two pulses into one long pulse. Yet, the two species use different criteria to recognize these merged pulses. While in *N. bivocatus* call recognition is based on pulse rate, female *T. viridissima* rely on the absolute durations of pulses and intervals, largely independent of the pulse rate (Schul, 1998).

Evolutionary implications

The calls of 25 *Neoconocephalus* species have been described qualitatively (Greenfield, 1990; Walker, 1975; Walker and Greenfield, 1983). The predominant temporal pattern is similar to that of *N. robustus*: pulses are repeated monotonously with a pulse rate of ~200–250 pulses s⁻¹ (at 25°C; Greenfield, 1990). The pulse rate of ~200 Hz in *N. robustus* is in the order of magnitude of maximum sustained firing rates of insect neurons (e.g. Franz and Ronacher, 2002). Such pulse rates are probably too fast to be encoded faithfully by the sensory system or to be analyzed by higher nervous centers. The absence of silent intervals, i.e. the absence of amplitude modulation, seems the only temporal characteristic that could be extracted from such a fast temporal pattern. Therefore, only a drastic reduction of pulse rate could lead to divergence of the communication system based on temporal cues. Because pulse rate is usually a 'static' call parameter (*sensu* Gerhardt, 1991), such large changes of pulse rate should be rare, as evidenced by the small number of species with pulse rates lower than 200 Hz.

N. bivocatus has circumvented this hurdle through a relatively small modification of the call generating mechanism. A delay introduced after every other closing movement of the forewings transforms a single pulse rate as in *N. robustus* into a double-pulse rhythm. This modification introduces a new temporal component into the call, effectively halving the pulse rate. In the case of *Neoconocephalus*, it would transfer the (double) pulse rate from 200 Hz down to below 100 Hz, and thus into a range that could be encoded and recognized by the sensory system.

The present study adds to a growing list of genera of acoustic insects and frogs in which call recognition mechanisms differ qualitatively between closely related species (Schul, 1998; Schul and Bush, 2002; Hennig, 2003). However, it is not clear which evolutionary mechanisms lead to this phenomenon (Schul and Bush, 2002) or if it is caused by the basic function of the nervous system underlying call recognition, as suggested by Hennig (2003). Broader comparative studies would be required to solve this problem.

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