Naturwissenschaften (2006) 93:500–505
DOI 10.1007/s00114-006-0135-9

SHORT COMMUNICATION

When males whistle at females: complex FM acoustic signals in cockroaches

Jérôme Sueur · Thierry Aubin

Received: 15 February 2006 / Revised: 23 May 2006 / Accepted: 23 May 2006 / Published online: 25 July 2006

Abstract Male cockroaches of the species *Elliptorhina chopardi* expel air through a pair of modified abdominal spiracles during courtship. This air expulsion simultaneously produces air and substrate-borne vibrations. We described and compared in details these two types of vibrations. Our analysis of the air-borne signals shows that males can produce three categories of signals with distinct temporal and frequency parameters. "Pure whistles" consist of two independent harmonic series fast frequency modulated with independent harmonics that can cross each other. "Noisy whistles" also possess two independent voices but include a noisy broad-band frequency part in the middle. Hiss sounds are more noise-like, being made of a broad-band frequency spectrum. All three call types are unusually high in dominant frequency (>5 kHz) for cockroaches. The substrate-borne signals are categorised similarly. Some harmonics of the substrate-borne signals were filtered out, however, making the acoustic energy centered on fewer frequency bands. Our analysis shows that cockroach signals are complex, with fast frequency modulations and two distinct voices. These results also readdress the question of what system could potentially receive and decode the information contained within such complex sounds.

Keywords Acoustic communication · Courtship · Two-voice system · Frequency modulations · Cockroach · (*Elliptorhina chopardi*)

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00114-006-0135-9 and is accessible for authorized users.

J. Sueur (✉) · T. Aubin
NAMC-CNRS UMR 8620,
Bât. 446, Université Paris XI,
F-91405 Orsay Cedex, France
e-mail: Jerome.Sueur@ibaic.u-psud.fr

Introduction

Birds and mammals are well known for the complex songs they produce when defending their territories or attracting a mate. These signals are mainly characterized by frequency modulations (FM) that may encode species, group, or individual specific information (Bradbury and Vehrencamp 1998; Holy and Guo 2005). In addition to this FM structure, some birds have the unique ability to produce two sounds independently and simultaneously (Suthers 1990). Such a "two-voice" phenomenon may encode an individual signature (Aubin et al. 2000).

Of all insects, the acoustic system of cockroaches is probably the least well studied. Hissing cockroaches of Madagascar (genera *Gromphadorhina* and *Elliptorhina*) produce sound by expelling air from their trachea through a pair of modified spiracles (Roth and Hartman 1967; Nelson 1979; Nelson and Fraser 1980; Fraser and Nelson 1984; Clark and Moore 1995). We focused our study on *Elliptorhina chopardi* (Lefeuvre, 1966), whose courtship display includes broad-band hisses as well as narrow-band whistles. Fraser and Nelson's (1982) short description of a limited number of signals indicated that these whistles contain two unrelated sets of harmonics, each with FM.

It is interesting to note that it is still unclear how the acoustic signals produced by cockroaches are received. Sound produced by walking animals can be transmitted via air or a solid. In cockroaches, there is no anatomical evidence of a tympanum to receive airborne sound. The subgenual organ, which is a mechanosensory organ found in legs, is able to detect low-frequency substrate-borne sound but also air-borne sound below 5 kHz (Guthrie 1966; Shaw 1994; Èokl and Virant-Doberlet 1997; Yager 2005). To detail the whistles of male *E. chopardi* further, we analyzed and compared both the air- and substrate-borne sound signals emitted during courtship display. This courtship signal could constitute one of the most complex acoustic signals among insects.

Materials and methods

Animals and observation setup

A colony of *E. chopardi* (Dictyoptera, Blaberidae) was reared in the laboratory and maintained at 26–27°C, 60–65% room humidity, and 12:12 h light–dark cycle. The light–dark cycle was shifted so the dark phase began at 1300 h. Males and females were housed separately after the fifth molt. Observations were carried out during the first 2 h of the dark phase under dim red light. One male and one female were placed for 15 min on a wooden platform (9×9×0.5 cm) that was changed between each trial. This platform was put on a stand (h=9 cm) enabling the cockroaches to move about freely. This setup avoided the echoes that would have occurred in a closed box. Only the recordings of males which successfully copulated were analyzed.

Signal recording, acquisition, and analysis

In a first series of recordings, a Sennheiser ME64 microphone (frequency response ±2.5 dB between 0.04 and 20 kHz) was held by a clamp on a movable stand, above the recording platform. It was thus possible to keep the microphone 1.5 cm above the male and track his movements.

In a second series, substrate-borne vibrations were detected with a miniature accelerometer Knowles BU-3173 (frequency response: flat between 0.1–3 kHz, ±2 dB for higher frequencies) that was fixed in the middle of the board. To allow accurate comparison between substrate and air-borne signals, the microphone was placed and fixed above the accelerometer. Both sensors were fixed but the cockroaches were free to move. The distance between sensors and cockroaches ranged between 1.5 and 10 cm.

The microphone and the accelerometer were connected to a Marantz PMD 670 digital recorder (44.1 kHz sampling frequency). To increase the signal to noise ratio, a frequency digital filter was applied to the signal using Goldwave. The spectrum of this filter was designed as the complement of a spectrum calculated in a signal section where only noise occurred. Filtered signals were then analyzed using Avisoft (Specht 2004) and Seewave (Sueur et al. 2006).

Call and intercall duration (CD, ICD) were measured on envelopes with a 0.001 s precision. Frequency parameters were measured on spectrograms using sliding short-term Fourier transforms (STFTs) with a 12.5% overlap (Hamming window length = 0.023 s). As signals naturally varied in their “noisiness”, call pureness was estimated using spectral entropy (SH). SH was calculated as the ratio of the geometric and arithmetic means of successive STFTs. Values of SH thus lay between 0 and 1, which, respectively, are indicative of a pure-tone signal and a random noise (Specht 2004). To quantify more precisely the distribution of frequency energy, the mean frequency spectrum of each call (STFT Hamming window length = 0.023 s) was divided into quartiles of energy: 25% (Q25), 50% (Q50), and 75% (Q75). To follow the variations of the dominant frequency (DF) along each call, the frequency of the highest energy peak was measured for 100 successive STFTs. The two spectrograms of each channel (microphone and accelerometer) were compared by using the cross-correlation algorithm of Avisoft (Specht 2004). This technique simultaneously analyses the frequency, amplitude, and time components of a signal by sliding the spectrogram (STFT length = 0.006 s, overlap 50%) of the air-borne signal along the time axis of the spectrogram of the substrate-borne signal (Khanna et al. 1997). For every offset position, the correlation coefficient of Pearson is computed. Only the maximum correlation value (r) is considered, where a value of 1 indicates similar signals.

Statistics

A Kruskal–Wallis test was used to compare the acoustic parameters describing different call categories and a post hoc Mann–Whitney test with Bonferoni correction was then used to test the difference between each call category. N gives the number of individuals and n the numbers of calls analyzed.

Results

Behavior

Courtship took place at a very short distance (<5 cm), the male and the female being almost always in contact (14 pairs observed). As soon as a female was detected, males regularly produced soft sounds by raising their abdomens. In addition to such sound emissions, male and female touched each other with their antennae and mouthparts, suggesting the use of contact pheromones.

Air-borne signals

Courtship duration, from the first call to copulation, was 239.15±152.75 s (N=16). Three call categories were identified: pure whistles (PW), noisy whistles (NW), and hisses (H) with, respectively, low, medium, and high SH (K–W χ^2=329.6, *df*=2, *p*<0.0001, all M–W tests between pairs with *p*<0.0001, Fig. 1, Table 1, S1). These categories differ by their duration, NW being the longer and H the shortest (K–W χ^2=38.6, *df*=2, *p*<0.0001, all M–W tests

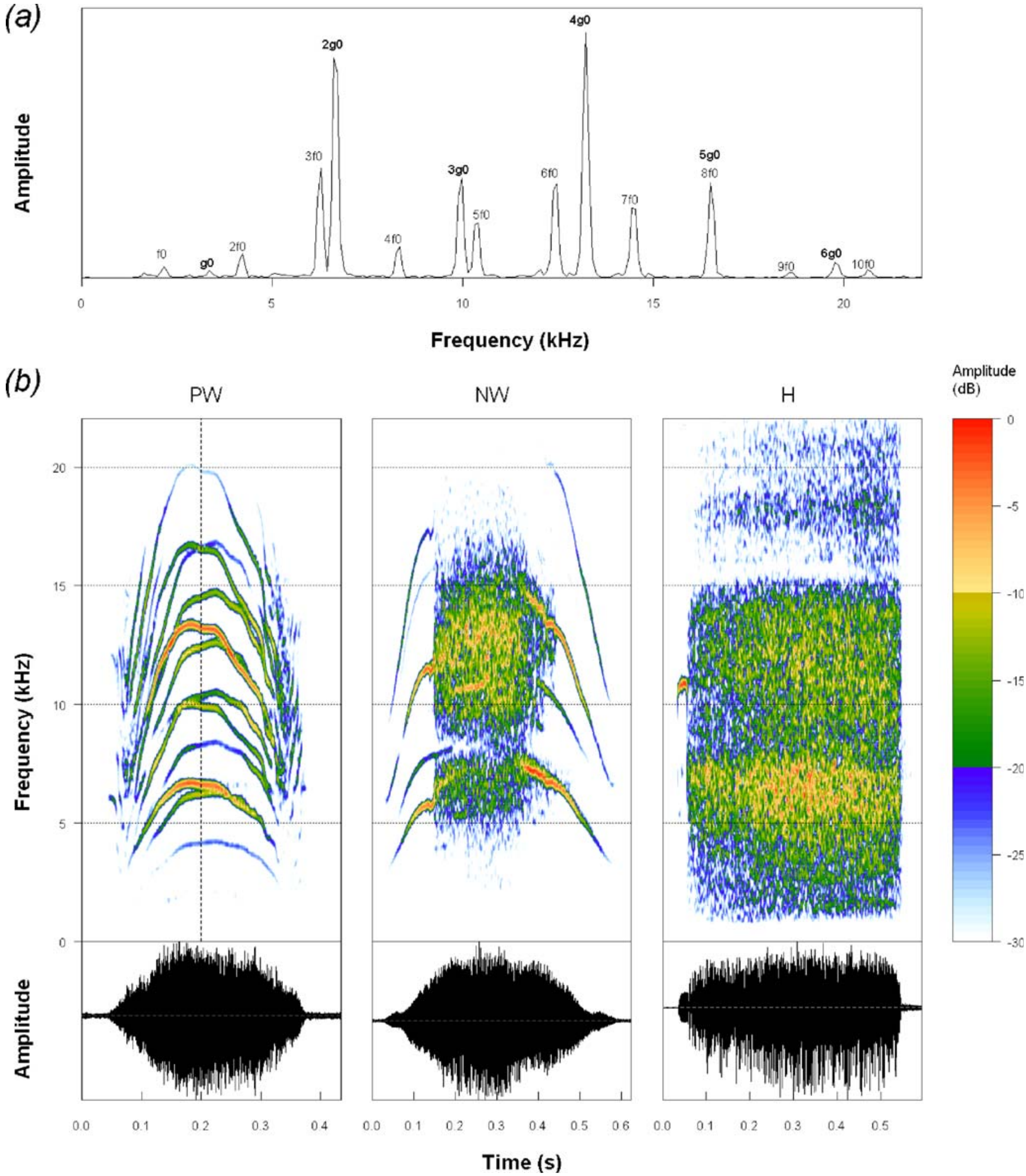

Fig. 1 Air-borne sound production by courting male of *E. chopardi*. **a** Spectral composition of PW showing two harmonic series (*i*f0 and *i*g0), calculated at the *vertical dotted line position* in **b**. **b** Oscillographic (absolute amplitude vs time) and sonographic (frequency vs time vs amplitude) representation. *PW* pure-whistle, *NW* noisy-whistle, *H* hiss. See S1 to hear these calls

Table 1 Temporal and frequency characteristics of acoustic signals produced by courting male of *E. chopardi*

	Air-borne signals			Substrate-borne signals		
Sample size	PW N=14; n=501	NW N=15; n=275	H N=11; n=44	PW N=8; n=149	NW N=7; n=103	H N=1; n=4
CD (s)	0.374±0.100; 0.020–0.590	0.410±0.082; 0.050–0.670	0.247±0.191; 0.010–0.600	0.288±0.091; 0.037–0.509	0.388±0.073; 0.230–0.684	0.270±0.099; 0.142–0.377
SH	0.52±0.10; 0.30–0.84	0.66±0.08; 0.40–0.79	0.75±0.07; 0.61–0.89	0.18±0.06; 0.07–0.34	0.26±0.09; 0.13–0.61	0.39±0.03; 0.34–0.41
Q25 (kHz)	6.30±0.99; 3.23–9.64	7.03±0.66; 4.86–9.86	7.65±0.97; 5.81–9.34	8.34±1.75; 2.62–10.85	8.47±0.13; 3.4–10.37	8.76±0.32; 8.48–9.04
Q50 (kHz)	8.16±1.52; 4.69–12.27	9.10±1.12; 6.93–11.41	10.26±1.10; 8.35–12.31	9.03±0.41; 2.88–11.11	9.16±1.13; 4.13–10.72	9.49±0.32; 9.21–9.81
Q75 (kHz)	9.98±2.00; 6.63–14.94	11.79±1.19; 8.44–14.08	12.94±1.25; 10.12–15.59	9.36±1.30; 3.66–12.18	9.84±0.82; 8.39–11.84	10.52±0.25; 10.16–10.68
Dfbeg (kHz)	5.46±1.54; 1.72–11.28	5.54±1.68; 1.55–11.92	7.65±3.00; 1.72–14.64	7.93±2.43; 1.20–13.3	7.99±2.48; 2.45–14.8	8.97±0.68; 8.39–9.86
Dfmid (kHz)	8.42±2.40; 3.83–15.59	8.99±2.24; 4.95–14.64	9.68±2.51; 4.95–15.37	9.05±1.57; 3.57–12.01	9.20±1.74; 4.04–11.84	8.94±3.97; 8.39–9.25
Dfend (kHz)	5.55±1.52; 1.46–12.01	5.58±1.69; 1.5–10.8	7.18±2.49; 1.85–15.33	8.00±2.44; 2.28–17.35	8.00±2.56; 2.36–17.78	8.29±1.93; 5.64–10.17

N number of individuals, *n* number of calls, *CD* call duration, *SH* spectral entropy, *Q25*, *Q50*, and *Q75* 25, 50, and 75% quartiles of spectral energy, *DFbeg*, *DFmid*, and *DFend* dominant frequency at the beginning, middle, and end of the call, mean±SD, min–max

between pairs with $p<0.0001$). ICD was 4.35±8.06 s (N=16, n=804).

PW signals were produced by 87.5% of males, NW by 93.75%, and H by 68.75%. Two independent harmonic series were detected in 63.5% of PW and in 85.5% of NW. When a single harmonic series was observed, it was impossible to state whether it resulted from the action of a single trachea opening or from both operating in perfect unison, i.e., time and frequency synchronization. Most of the spectral energy was higher than 5 kHz as shown by the spectral quartile values. PW showed significantly lower values for spectral quartiles than NW and the latter showed lower values than H (K–W χ^2=133.6, df=2, $p<0.0001$, all M–W tests between pairs with $p<0.0001$).

The frequency structures of PW and NW were complex, independent harmonic series crossing each other and showing distinct rising/falling time values. PW were made of an overall frequency rising from the beginning to the middle of the call and then of a frequency falling. NW followed the same general pattern but the middle of the call was characterized by a broadband spectrum without clear harmonic structure. H calls were made of a similar noisy broadband spectrum (Table 1). Some FM could be observed at the beginning or at the end of H calls. The dominant frequency was lower in the PW than in the NW and the H.

Substrate-borne signals vs air-borne signals

Signals recorded, both through the substrate and the air, showed the same overall FM pattern. However, other frequency bands aside from the dominant one were partially or totally absent. SH was lower for PW and NW but not for H (Table 1, PW: W_x=6311, $p<0.0001$; NW: W_x=3519, $p<0.0001$; H: W_x=10, p=0.69). The two sets of harmonics were more difficult to detect in substrate-borne signals: they were only detected in 45.5% of PW and in 30.2% of NW. In addition, the dominant frequency showed the same overall variation pattern but with higher values at the beginning and the end (DFbeg and DFend) of the PW and NW calls. The maximum correlation (r) between air and substrate-borne signals gave values less than 0.5 (Fig. 2).

Discussion

Gromphadorhina and *Elliptorhina* species are the only insects known to emit courtship sound by expelling air (Roth and Hartman 1967). We report in this study that *E. chopardi* is able to produce at least three types of signal, categorized by their spectral entropy and duration (PW, NW, and H). These call categories could encode different types of information and/or be related to the level of male

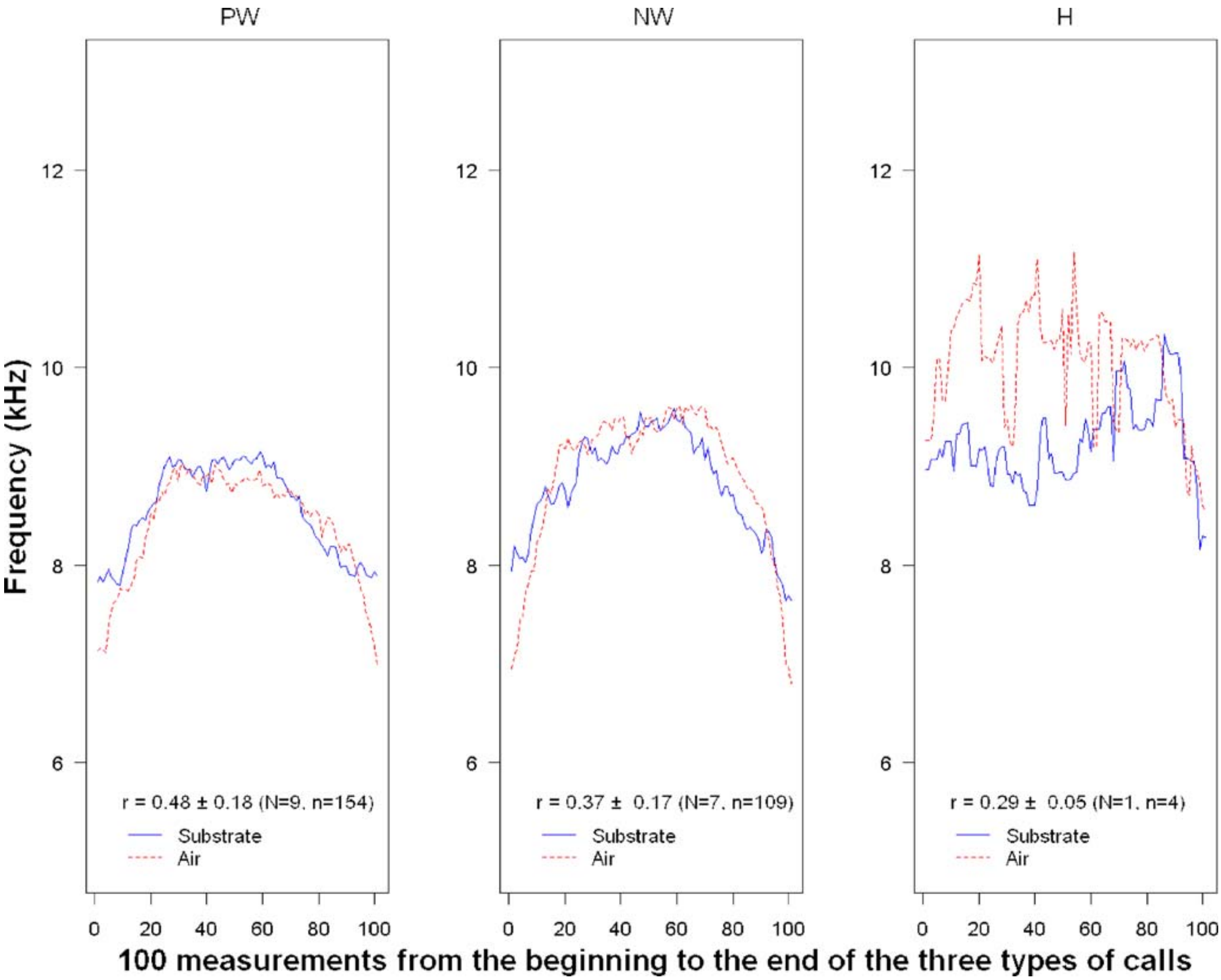

Fig. 2 Comparison of the variation of the dominant frequency of air and substrate-borne calls. Mean±SD of the correlation coefficient (*r*) between the two transmission channels is given for each type of call. *PW* pure-whistle, *NW* noisy-whistle, *H* hiss

motivation to copulate. The two most often calls emitted (PW and NW) sound like the whistles produced by birds or mammals. These signals demonstrate very complex FM air-borne vibrations with two independent harmonics series that can overlap and even cross each other. Cockroaches and birds seem to be the only animals able to produce two distinct harmonic series by independent acoustic sources. Instead of revealing a complex information system, the frequency composition of the cockroach's signal could simply be an epiphenomenon resulting from the modified tracheal system. In *G. portentosa* as in *E. chopardi*, the trachea of the sound-producing spiracle is constricted proximally but elongated distally and closed by a valve (Nelson 1979). If three muscles attached to the valve can be used to control sound amplitude, it is less clear how frequency may be actively modified. We can hypothesize that a controllable constriction in the air passage could produce variations in pitch: the higher the pressure, the higher the frequency. During intense expiration, an excess of air flow can probably overdrive the resonant properties of the trachea. Such a nonlinear phenomenon can generate chaotic oscillations leading to the noisy parts of calls.

Signals can be transmitted through air and also via the substrate. PW and NW signals transmitted through the substrate are characterized by a less complex frequency structure, but demonstrate a similar overall rising-falling FM pattern. The differences between the substrate- and air-borne vibrations may be due to the individual sensitivities of the microphone and the accelerometer, in particular the narrower frequency sensitivity range of the accelerometer. The use of sensors covering a broader frequency bandwidth and with a higher sensitivity, like a laser vibrometer, might clarify or even reduce these dissimilarities. In addition to this, wood and air present two very distinct propagation media for transduction vibrations.

Acoustic transduction would be more efficient between the trachea and air than between the trachea and substrate.

It has yet to be shown which transmission channel cockroaches communicate through and likewise their receptor system is still not clearly identified. The subgenual organ of other cockroach species has been shown to receive air-and substrate-borne vibrations lower than 5 kHz in frequency (Shaw 1994; Èokl and Virant-Doberlet 1997; Yager 2005). Our study reports frequencies much higher than this lower limit. Neuronal recordings of the subgenual receptor cells may yet demonstrate exceptional sensitivity to high frequencies. The Johnston's organ, a mechanoreceptor embedded in the antenna, might play a role in near-field sound detection but this organ is usually tuned to low frequencies (Robert and Göpfert 2002). Structures like trichoid sensilla could detect air motion associated with air expulsion and thus participate to signal reception. Further investigation, including observations in natural conditions and playback experiments, are now needed to fully understand the biological significance of these signals.

Acknowledgements We thank Gérard Dutrilleux for maintaining the electronic recording system, Julie Chébaux for data acquisition, Anne Cherpin for the advice in rearing cockroaches, Christine Marlet for taking care of insects, Meta Virant-Doberlet and Elizabeth Tuck for critical reading of the manuscripts. We gratefully acknowledge Knowles Company for providing miniature accelerometers. We thank Charlie Henry and four other reviewers for their helpful comments.

References

Aubin T, Jouventin P, Hildebrand C (2000) Penguins use the two voice system to recognize each other. Proc R Soc Lond B 267:1081–1087

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates, Sunderland, Massachusetts

Clark DC, Moore AJ (1995) Variation and repeatability of male agonistic hiss characteristics and their relationship to social rank in *Gromphadorhina portentosa*. Anim Behav 50:719–729

Čokl A, Virant-Doberlet M (1997) Tuning of tibial organ receptor cells in *Periplanetaamericana* L. J Exp Zool 278:395–404

Fraser J, Nelson MC (1982) Frequency modulated courtship song in a cockroach. Anim Behav 30:627–628

Fraser J, Nelson MC (1984) Communication in the courtship of a Madagascan hissing cockroach. I. Normal courtship. Anim Behav 32:194–203

Guthrie DM (1966) Sound production and reception in a cockroach. J Exp Biol 45:321–328

Holy TE, Guo Z (2005) Ultrasonic songs of male mice. PLoS Biol 3:e386

Khanna H, Gaunt LL, McCallum DA (1997) Digital spectrographic cross-correlation: tests of sensitivity. Bioacoustics 7:209–234

Nelson MC (1979) Sound production in the cockroach *Gromphadorhina portentosa*: the sound-producing apparatus. J Comp Physiol A 132:27–38

Nelson MC, Fraser J (1980) Sound production in the cockroach, *Gromphadorhina portentosa*: evidence for communication by hissing. Behav Ecol Sociobiol 6:305–314

Robert D, Göpfert MC (2002) Acoustic sensitivity of fly antennae. J Insect Physiol 48:189–196

Roth LM, Hartman B (1967) Sound production and its evolutionary significance in the Blattaria. Ann Entomol Soc Am 60:740–752

Shaw SR (1994) Detection of airborne sound by a cockroach vibration detector: a possible missing link in insect auditory evolution. J Exp Biol 193:13–47

Specht R (2004) AVISOFT-SAS Lab Pro. Avisoft, Berlin

Sueur J, Aubin T, Simonis-Sueur C (2006) Seewave. Université Paris XI-MNHN, Paris

Suthers RA (1990) Contributions to birdsong from the left and right sides of the intact syrinx. Nature 347:473–477

Yager DD (2005) Cockroach homologs of Praying Mantis peripheral auditory system components. J Morph 265:120–139