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Sound Production in the Cockroach, *Gromphadorhina portentosa*: Evidence for Communication by Hissing

Margaret C. Nelson[1]* and Jean Fraser[2]

[1] Department of Neurobiology, Harvard Medical School, Boston, Massachusetts 02115, USA
[2] Department of Psychology, Brandeis University, Waltham, Massachusetts 02154, USA

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Summary. 1. Sound production of the giant Madagascar cockroach, *Gromphadorhina portentosa,* was examined by behavioral and acoustical methods in order to determine the functions of the hisses produced by this species.

2. *Gromphadorhina* is able to produce audible hisses from a pair of modified spiracles. Adult males hiss in three social contexts: during aggressive encounters, during courtship (when two types of hisses are discernable), and during copulation. Adults and nymphs of both sexes also hiss when disturbed (Figs. 2 and 3).

3. There are reliable differences among hisses emitted in these social contexts which depend on several features: the shape of the amplitude envelope (Fig. 4), the relative loudness (Table 1), and the temporal characteristics both of single hisses and of hiss trains (Table 1 and Fig. 4).

4. In both courtship and aggression, hissing accompanies characteristic, stereotyped behavior patterns (Figs. 5 and 7); during aggressive encounters between males, hissing is predictive of winning (Fig. 6).

5. Males which have been silenced by occlusion of the specialized spiracles carry on apparently normal courtship, but they are unsuccessful in copulating due to a lack of receptive behavior by the female (Fig. 8).

6. Playback of recorded courtship hisses during courtship of females by silenced males leads to receptive behavior by females, and to normal rates of copulation (Fig. 8).

7. Our evidence supports the hypothesis that *G. portentosa* has evolved a system of communication in which hisses serve as auditory social signals.

Introduction

In 1938 Chopard described a unique ability to hiss shown by cockroaches of the genus *Gromphadorhina,* endemic to Madagascar. Since that time a handful of investigators have remarked on this capacity, which depends on the forceful expulsion of air from a modified spiracle (Dumortier, 1965; Nelson, 1979a). Yet there has been no careful analysis of the functions of these sounds, nor, indeed, of the sounds themselves. We have investigated the sound production of *G. portentosa,* an extremely large member of the genus, and have gathered evidence that the animal uses the sounds it produces for intraspecific communication. To establish this, we asked (a) whether characteristic hisses occur in specific social and nonsocial contexts, (b) whether the acoustical characteristics of the sound vary systematically from one context to another, and (c) whether experimental manipulation of sound production and reception affects the behavior of either the sender or the recipient or both. We report that there are several acoustically distinct hisses, each of which accompanies a specific class of social interactions or environmental stimuli. When animals are prevented from hissing in a given social encounter, the outcome of the interaction is affected, but when recorded sounds characteristic of that interaction are played for such animals at the appropriate time, the interaction appears normal in most respects.

Sparse information on sound production in *Gromphadorhina* is available in the literature. Most of the species in the genus apparently do hiss under several conditions. Hisses elicited by rough handling have been most widely observed: in *G. brunneri* (Dumortier, 1965; Ziegler, 1972), in *G. portentosa* (Roth and Hartman, 1967; personal observation), in *G. laevigata* (Chopard, 1950), in *G. javanica* (Roth and Hartman, 1967), and in *G. chopardi* (Roth and Hartman, 1967; personal observation). Several of these authors found

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* Present address: Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA

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that attempts to feed *Gromphadorhina* to various predators – none native to Madagascar – led to vigorous hissing. In keeping with this anecdotal tradition, we have found that being half-swallowed by a gecko is by far the most effective stimulus for hissing. Hissing is also reported to occur, in males only, during courtship and in defense of territory (Dumortier, 1965, and Ziegler, 1972, for *G. brunneri;* Barth, 1968, for *G. portentosa*).

It has become increasingly clear in recent years that a number of species of cockroaches have a relatively complex social organization (Ewing, 1972; Ritter, 1964; Ziegler, 1972). Ziegler surveyed the sexual and territorial behavior of *G. brunneri* and found that under laboratory conditions they lived in loosely organized communities comparable to those described for *Nauphoeta cinerea* by Ewing (1972). Females were almost wholly gregarious; males showed some territorial behavior, in that some of the males in a group showed 'constancy of space' and defended a small area around a particular spot, often an elevation in their tank. Dominant males were more likely to attempt to copulate with females than were subordinate males that did not hold a territory (Ziegler, 1972; personal observation).

We have found that *G. portentosa* has evolved a sound-signaling system that appears to serve for communication and for maintenance of social structure. Here we describe some of the components of social displays in this species, show how hissing is incorporated into these displays, and describe the acoustical characteristics of the hisses.

Materials and Methods

Gromphadorhina portentosa is a large (adults 5–9 cm, 6–24 g), apterous, false-ovoviviparous cockroach. The minimal gestation period for females in our colony was 60 days. The nymphs undergo six (rarely, seven) molts, reaching adulthood in the seventh instar; time to maturity under our conditions is about five months, and adults may live for two or more years. The animals used in this study were descendants of animals obtained from Louis Roth (U.S. Army Natick Laboratories).

The colony was maintained at 25° C and approximately 65% relative humidity. Unless otherwise noted, animals were kept under a shifted light-dark cycle (12 h–12 h) with 'sunset' at 12 a.m. There was a constant supply of water and dry dogfood supplemented by fresh fruits and greens. Nymphs were housed separately from adults; males and females were housed separately after the fifth (penultimate) molt.

Observations were carried out during the first few hours of 'night' under dim red light provided by a G.E. 40-W red light bulb. For observations of normal courtship and aggression, the observation chamber was a Lucite box ($15 \times 30 \times 10$ cm) bisected by a removable opaque partition. Animals were always transferred to this test chamber 24 h before a test began, in order to allow acclimatization. Observations began with removal of the partition and continued for at least 15 and no more than 60 min. The observer used a tape recorder for notetaking.

Aggressive Behavior. To establish criteria for aggression levels and incidence of hissing, we observed 20 young adult males of comparable age and size (age two weeks since final molt at onset of observations, body weight 5–7 g) in paired aggressive interactions, using a Latin square design. The death of one male during testing resulted in a total of 182 encounters. Three days prior to the first observation, all males were removed to individual isolation chambers ($10 \times 10 \times 6$ cm) where they were maintained between matches. No animal was tested more than once in three days, to reduce possible after-effects of winning or losing an aggressive encounter (Ewing and Ewing, 1973). To construct an ethogram, we made detailed written and taped commentaries of 18 such encounters, each lasting 30 min; these were analyzed to establish the sequence of behavioral acts during aggression.

Courtship Behavior. To establish an ethogram of courtship, we observed 25 males and 25 females. Males were drawn at random from the colony tanks; females were drawn from virgin stock maintained in isolation from males since the sixth instar. Each observation lasted for 30 min.

Videotaping. Some aggressive and courtship encounters were recorded on videotape (Sony Videocorder EV-210) and played at slow speed for detailed analysis of behavior. Courtship sequences, carried out in a clear Lucite container, were videotaped from below (ventrally). The video camera (Sony DXC-2000) was equipped with an extra lens (1 diopter) which made it possible to film a 9×15 cm field with excellent resolution.

Muting and playback. 1) Animals: 60 males tested were, each with three virgin females drawn at random from all-female colony tanks. Fifteen untreated males made up the 'normal' group. Thirty males had the valves of both specialized spiracles glued shut with cyanoacrylate glue, after they had been cooled to enable handling. Fifteen of these (the 'mute' group) were observed during courtship without intervention. The other 15 (the 'playback' group) were given replacement therapy in the form of a recorded sequence of courtship hissing, which was played whenever they made an attempt to copulate (see Results for a full description of courtship). A fourth group of 15 males (the 'sham' group) served as a control for possible side effects of the muting operation. In these, glue was applied to the spiracle valves as for muting, but the flap of the valve was not glued shut.

2) Test conditions: All males were isolated in individual plastic chambers ($10 \times 10 \times 6$ cm) for three days before testing. They were maintained under a 14 h–10 h light-dark cycle with 'sunset' at 10:30 a.m. Each animal was moved to its test chamber 24 h before testing; the test chambers were cylindrical Lucite cages, 20 cm in diameter by 13 cm high, with wire-mesh floors. The observations, each lasting 15 min, were carried out in a quiet, anechoic room under dim red light provided by a single 40-W G.E. red light bulb. Temperature was maintained at 26°–27° C.

3) Sound recording and playback: The playback signal was a sequence of type-2 courtship hissing (see Fig 1), which had elicited standing from the female. Hissing was recorded with a Bruël and Kjaer 4136 $^1/_4$-inch microphone and a GenRad 1560 preamplifier on a TEAC 2300S tape deck at $7^1/_2$ ips. Recording was carried out in a soundproof, anechoic chamber. (The chamber was 5 ft high with a pentagonal cross-section, each side 46 inches long, constructed of $^3/_4$-inch plywood. Interior insulation consisted of an outer layer of 5-inch fiberglass insulation material, and an inner layer of 5-inch fingerfoam. Sound attenuation was -60 dB at 5 kHz). The mean sound level of the courtship hissing

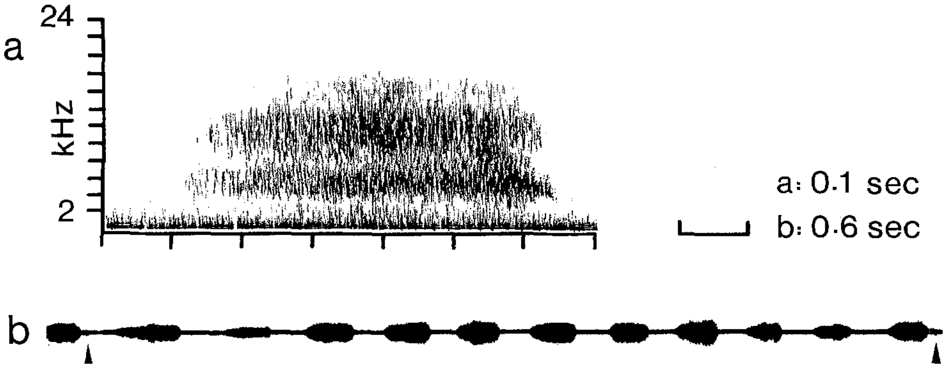

Fig. 1a and b. Sonagram (**a**) and oscillogram (**b**) of the courtship sounds used for playback. Both (**a**) and (**b**) were taken from the 45-min tape which was heard by animals in the playback group; **a** sonagram of the first hiss in the series; **b** oscillogram of the complete sequence of hisses; the *arrowheads* indicate the beginning and end of the tape loop from which this tape was made

emitted by the male used for recording was measured at a distance of 1.5 cm from the male (the approximate distance from the female during thrusting) using a Bruël and Kjaer 2209 sound-level meter; the mean sound pressure level was 61 dB.

The recorded sequence of hissing which was selected for playback was made into a 7.5-s tape loop, and this was used to record a continuous 45-min tape of courtship hissing. This stimulus tape was played on a TEAC tape deck, through an audio amplifier (Realistic SA-101), and finally through a piezoelectric tweeter. All sound equipment other than the loudspeaker was located in a room adjacent to the test room. The loudspeaker was centered facing upward beneath the test cage, 3 mm from its wire-mesh floor; the cage was held separately in midair by a padded clamp attached to a vertical support, so that loudspeaker and cage were not in contact. The amplitude of the sound stimulus was adjusted to provide a signal with a mean sound level of 61 dB SPL when measured 1.5 cm above the speaker. During playback experiments, all the sound equipment was turned on for the duration of the observation, with the exception of the loudspeaker, which could be controlled independently by the observer via a silent switch. Whenever the male being tested began a copulation attempt, the observed switched on the loudspeaker and left it on until the copulation attempt ended, when the sound was immediately switched off.

Acoustical Analyses. We recorded hisses in a quiet room on a Sanborn/Hewlett Packard 3900 tape recorder at a tape speed of $7^{1}/_{2}$ (passband 50–32,000 Hz) with a Bruël and Kjaer $4136^{1}/_{4}$-inch condenser microphone and a GenRad 1560 preamplifier (frequency range of 50 Hz to 70 kHz). The microphone was normally handheld 1 cm from the animal. Tapes obtained in this way were used later for several kinds of analyses. We visualized the frequency range and temporal variation in frequency with a Kay 6061B Sonagraph. All sonagrams were made on wide-band setting with a frequency range of 160 Hz to 16 kHz; the effective range was expanded to 32 kHz by playing taped hisses at one-half the recording speed. We determined amplitude envelopes and interhiss intervals from oscillograms of taped hisses. We also determined the frequency spectra of selected hisses by Fourier analysis, using a commercial Fast Fourier Transform program (Digital Equipment Corp. Users' Service) and a PDP-12 computer. Hisses were recorded for Fourier analysis at 60 ips, and played back at $3^{3}/_{4}$ ips; a Krohn-Hite 3550 bandpass filter limited the playback signal to between 62.3 Hz and 3.12 kHz (corresponding to a range of 1–50 kHz for the recorded signal). The playback signal was digitized at twice the upper band limit. Blocks of 512 points of digitized data were multiplied by a Hamming window, and the power spectra were calculated. Four spectra, derived from successive 20-ms samples from a single sound, were averaged and displayed linearly; for each hiss, we sampled from the region of peak amplitude.

Amplitudes of hisses were measured during behavioral observations with a GenRad 1565b sound-level meter. In order to avoid disrupting ongoing behavior, readings were taken with the microphone held approximately 5 cm from the animal. Figures given are the A-weighted sound level (dB *re* 20 μN/m^2).

Results

General Characteristics of Sound Production

All of the hisses recorded in these studies had a broad frequency spectrum as indicated both by sonagrams (Fig. 2) and by Fourier analysis (Fig. 3). Frequencies below 2 kHz contributed little to the power spectra. There were slight differences in frequency spectrum from animal to animal (Fig. 2) and among kinds of hisses from a single animal (Fig. 3); these depended partly on the size of the animal (the peak frequency shifted downward for larger animals) and partly on the amplitude of the sound (the peak frequency shifted upward for louder hisses). Sonagrams revealed, however, that the frequency spectrum remained essentially the same throughout a given hiss.

Types of Hisses: Contexts and Characteristics

At least four broad categories of hisses could be distinguished on the basis of behavioral contexts and acoustical characteristics.

Disturbance Hissing. Adults of both sexes, and nymphs starting at the fourth instar, hissed upon receiving any of a variety of sudden or disruptive stimuli of several modalities. These included sudden onset of light, rapid movement of edges or shadows, vibration of the substrate, or handling of the animal. Al-

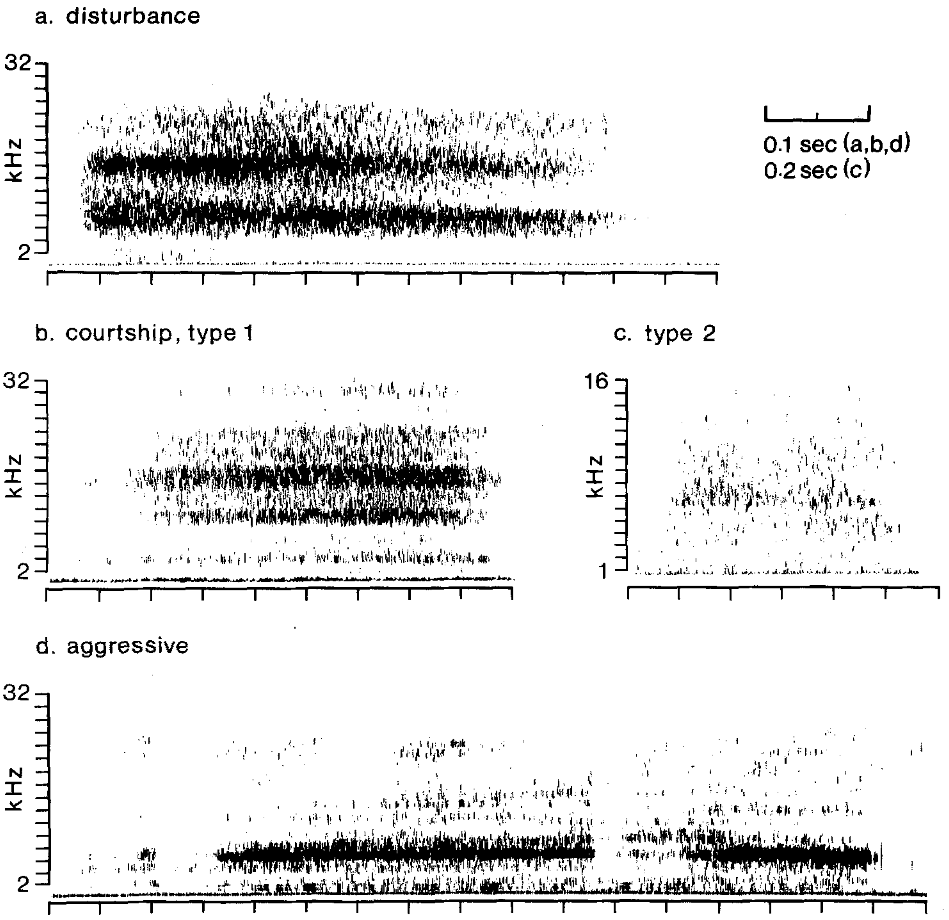

Fig. 2a–d. Sonagrams of hisses emitted by four specimens of *G. portentosa*: **a** disturbance hiss emitted by a 10.9-g male; **b** type-1 courtship hiss emitted by a 6.2-g male; **c** type-2 courtship hiss emitted by a 6.4-g male; **d** aggressive hiss emitted by an 8.2-g male

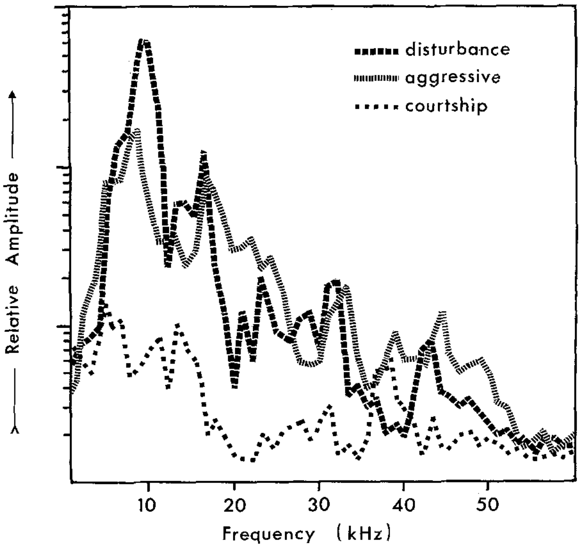

Fig. 3. Frequency spectra of disturbance, aggressive, and type-1 courtship hisses produced by a single adult male. Amplitude (log scale) is relative to a constant-intensity signal (uncalibrated)

though disturbance hisses were most frequently elicited by nonsocial stimuli, they were occasionally emitted by unreceptive females when approached by a courting male. Stereotyped postures accompanied hisses elicited by focal tactile stimulation. Lateral stimulation, which led to tilting of the body to the stimulated side, elicited unilateral hissing on this side. Repeated or especially strong stimuli elicited trains of disturbance hisses; under sufficient provocation the disturbed animal would break into a run and make several circuits of its tank while hissing repeatedly.

Disturbance hisses were distinguished by their amplitude, the highest recorded for any class of hisses; Table 1 summarizes the amplitude and temporal characteristics of hisses. Recorded sound levels ranged from 70 to 87 dB SPL at a distance of 5 cm from the animal. The amplitude evelope was also distinctive, with a sharp rise to maximum amplitude and a slow decline thereafter (Fig. 4a). While there was

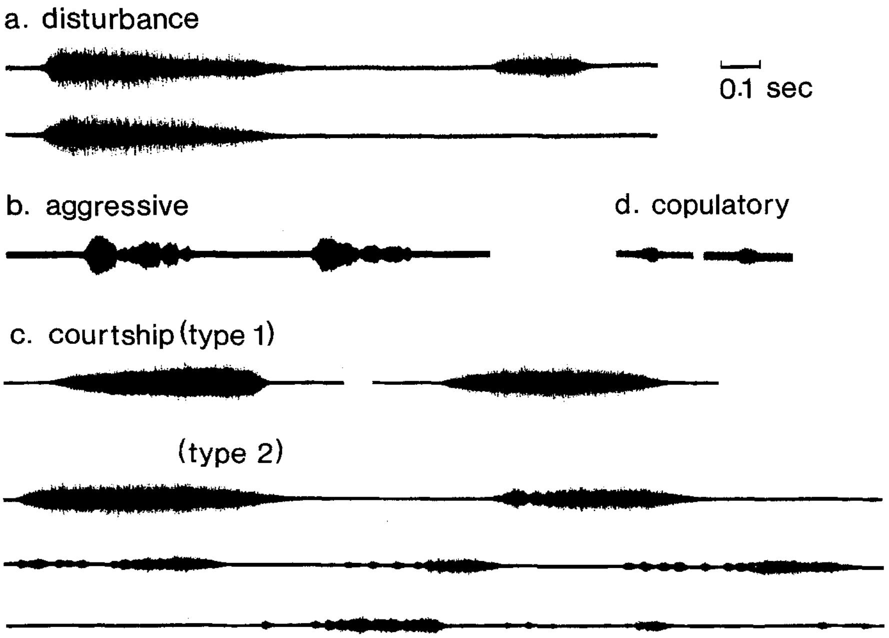

Fig. 4a–d. Oscilloscope tracings of hisses recorded in different contexts. All hisses were emitted by adult males; **a** hisses elicited by pinching the animal's leg; **b** hisses emitted by a territorial male when confronted by an intruding male; **c** (type-1): hisses emitted by a male while posturing during courtship (see Fig. 8); (type-2): hisses emitted by a male while thrusting during courtship (see Fig. 8); **d** hisses emitted by a male during copulation. Amplification of the signals was uncalibrated but increased from (**a**) to (**d**)

some variability in amplitude envelope from one sample to another, the rapid rise time was still evident after averaging a number of samples (maximum amplitude was reached 16% ± 0.02% of the way through the hiss; $\bar{x} \pm$ SEM, $n=20$). The average duration of disturbance hisses was 0.58 s. When an animal emitted a train of disturbance hisses the intervals between hisses were variable, without consistent temporal structure.

Aggressive Hissing. Adult males, particularly after a period of isolation, engaged in vigorous fighting with other males, as outlined in Fig. 5. Fighting began only after males came into antennal contact with one another (1). When fighting followed antennal contact, it was most frequently initiated by butting (2), in which one animal charged and rammed his massive pronotum (which bears two humps in adult males) against his opponent. In butting, the attacker often pushed his opponent for several centimeters or flipped him over completely.

Butting was most often followed by one of two clusters of behaviors; in each case two or more behaviors alternated rapidly and repeatedly. The first, less frequent cluster, performed in contact with the opponent, consisted of biting the opponent on the back, legs, or antennae (3); or antennal fencing with the opponent (4), in which one or both animals moved their antennae rapidly with small, jerky excursions in the horizontal plane. The second, more frequent cluster (5 and 6), performed out of contact with the other animal, consisted of posturing, in which the animal stood with his body held high off the ground and abdomen curved upward while extending the pregenital segments; or abdomen-thrashing (6), in which the animal stood or walked about with his thorax held high off the ground and thrashed his abdomen from side to side repeatedly, occasionally slapping it against the ground in passing.

Ninety-five percent of the hissing observed during aggressive encounters occurred during abdomen-thrashing displays, although these displays often occurred without sound production (60% of the time). Abdomen-thrashing displays often alternated with posturing (5). During aggressive encounters (in contrast to courtship encounters), this display occurred without sound production unless the animals engaged in pseudocopulatory behavior, i.e., courtship behavior directed toward the other male; When this happened, posturing was accompanied by courtship hissing. The response to attack by another male varied from a return of the attack in kind, to assumption of a submissive stance with the body flattened against the ground (7). In those encounters that ended in a clear win (see below), the winner ended the interaction with an abdomen-thrashing display in 90% of the encounters.

Aggressive encounters did not always involve hiss-

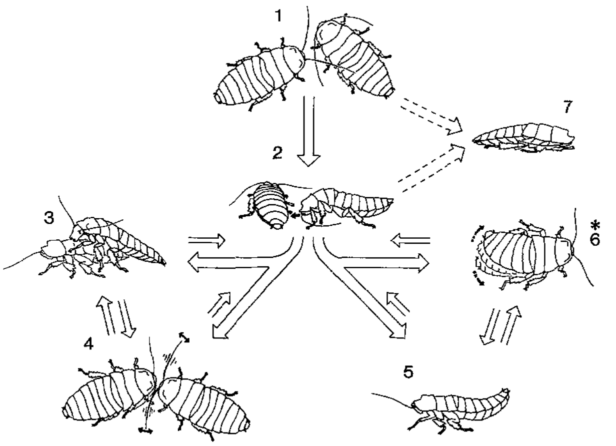

Fig. 5. Aggressive behavior in *G. portentosa*. *Arrows* indicate the typical sequence of events, based on observations of 18 encounters; *1*, Aggressive behavior is initiated by antennal contact; *2*, this is usually followed by an attack in the form of butting. Two clusters of behavior on the part of the attacking animal may follow butting: *3*, biting on the legs, back, or antennae; and *4*, fencing with the antennae; or *5*, posturing; and *6*, abdomen-thrashing (which may be accompanied by hissing). Within each cluster, both behaviors alternate with each other and with butting. *7*, The attacked animal, if it does not return the attack in kind, may assume a submissive posture following initial contact or butting. The *asterisk* indicates the behavior with which hissing is associated

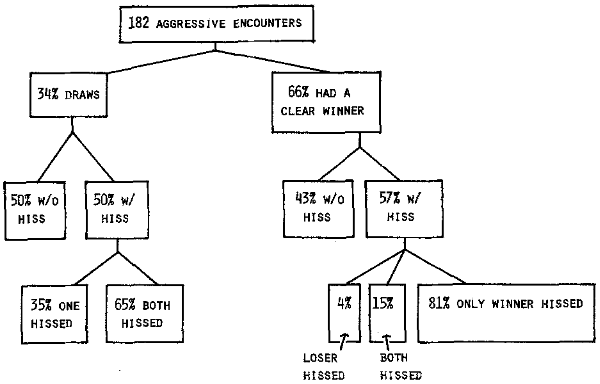

Fig. 6. Distribution of aggressive hissing in a series of 182 aggressive encounters as a function of the outcomes of the encounters. Fights were scored as being draws (34%) or as having clear winners (66%); within these categories, encounters were sorted according to whether hissing was absent (*w/o hissing*) or present (*w/ hissing*), and the identity of the animal hissing was noted

ing; more aggressive animals, however, were more likely to hiss. We ranked levels of aggressiveness on the basis of a cluster of behavior patterns that had predictive value for the outcome of aggressive encounters. Matches were scored as either clear wins or draws, and animals were assigned to the 'clear win' category by reference to three criteria:

a) presence of unambiguous attack (the 'winner' butts, bites, pushes, antennal-fences and/or chases the 'loser');

b) degree of movement (the winner moves freely within the test box, but the loser remains immobile); and

c) posture (the winner stands with body raised, head down, and abdomen off the ground or raised upward, while the loser flattens his body against the ground with all appendages retracted under the body).

Figure 6 charts the outcomes of 182 paired aggressive encounters which were judged by these criteria. In those matches which had a clear winner (66%), hissing occurred in 57% of the matches. Within this subset, only the winner hissed during the observation period in the great majority of matches (81%), the loser alone hissed in only 4% of them. The identity of the animal emitting sound was evident both from the direction of the sound and from the fact that abdominal compression accompanies sound production.

The amplitude of aggressive hisses fell between those of courtship and disturbance hisses (Table 1). The amplitude envelope shape varied considerably, but an abrupt onset and slow fluctuations in amplitude during the hiss were typical (Fig. 4b). These hisses did not differ significantly in length from disturbance hisses.

Table 1. Hiss amplitude (SPL)[a] and hiss duration[b]

Hiss category	Amplitude (dB re 20 μN/m²)	Duration (s)
Disturbance	70–87 dB	0.58 ± 0.03 s ($n=75$)
Aggressive	55–62 dB	0.60 ± 0.03 s ($n=75$)
Courtship, type 1	45–55 dB	0.54 ± 0.02 s ($n=75$)
Copulatory	<40 dB	0.06 ± 0.004 s ($n=21$)

[a] Sound pressure level (SPL): numbers indicate range, based on at least 20 readings (5 in the case of copulatory hisses); hisses in each category differ significantly in sound level from hisses of all other categories ($P < 0.001$)

[b] Durations of hisses based on oscillograms: numbers are mean ± standard error of the mean. Hisses in the first three categories do not differ significantly from one another in length; copulatory hisses differ significantly from all other categories in length ($P < 0.001$)

Courtship Hissing. Adult males and females displayed a characteristic sequence of behavior during courtship which is shown diagrammatically in Fig. 7. Either the male or the female could make the initial contact (1). This most frequently led to mutual antennation (2), in which the antennae made wide, slow sweeping movements laterally. This usually elicited posturing by the male (3), who would stand with thorax raised high off the ground and abdomen curved upward and extended; the phallomeres were often partially

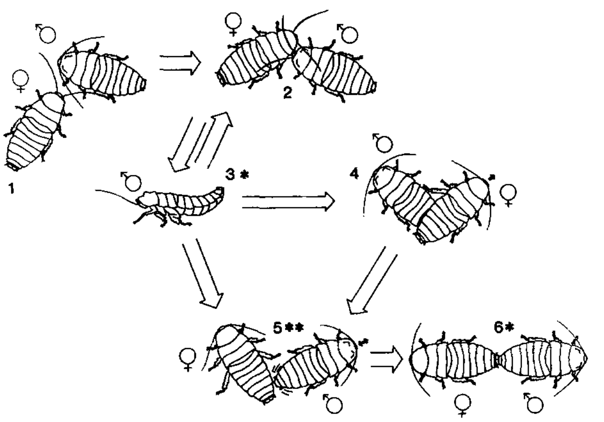

Fig. 7. Courtship behavior in *G. portentosa*. *Arrows* indicate the typical sequence of events, based on observations of 25 encounters; *steps 2–5* are commonly repeated several times before successful copulation. *Asterisks* indicate the behaviors with which hissing is associated; *1*, initial approach by either animal; *2*, mutual antennation; *3*, male postures with extended abdomen, and may hiss (type-1 courtship hiss); *4*, female 'crosses over' male (drags her abdomen over his); *5*, copulation attempt by male: male thrusts while hissing (type-2 courtship hiss); and *6*, copulation (male may hiss)

extruded at this time. During courtship this display was closely associated with sound production; 55% of hissing (type 1 – see below) during courtship occurred during posturing, and 42% of posturing was accompanied by hissing. A hiss recorded at this time is shown in the first portion of Fig. 4c.

Posturing (3) frequently led to 'crossing over' by the female, who would crawl over the male's back, dragging her abdomen across his. This frequently elicited a copulation attempt consisting of 'thrusting movements' (5) in which the male inserted the tip of his abdomen, phallomeres extruded, under the female's side while making a complex sideways/lengthways thrusting motion, at the same time gradually shifting his body to assume an opposed position (abdomens tip to tip). A train of hisses (shown in second portion of Fig. 4c) invariably accompanied this behavior. Videotapes filmed from beneath the animals revealed that such hisses were coterminous with thrusting episodes but were not directly coordinated with individual contractions or extensions of the abdomen.

Females which were receptive, as defined by eventual copulation, responded to thrusting by standing still with the legs extended laterally, body close to the ground, and abdomen flexed downward at the tip (equals 'standing'). Unreceptive females responded to thrusting by moving away from the male. Copulation (6), when it occurred, was in the opposed position and lasted an average of 20 min.

During a normal courtship, the animals usually went through these interactions a number of times. In observations of 25 pairs, males averaged 7.2 ± 1.6 copulation attempts per 30-min observation period. The animals actually copulated in 20% of the pairings.

Hisses emitted during courtship fell into two classes, which shared certain characteristics. Hisses of the first type, which usually accompanied posturing, occurred singly or at long and irregular intervals (6–10 s). The amplitude envelope typically rose slowly to peak amplitude, reaching maximum amplitude just before the hiss ended (Fig. 4c). The time at which the maximum amplitude was reached varied somewhat, but the average shape was characteristic (maximum amplitude was reached $67\% \pm 0.03\%$ of the way through a courtship hiss; $\bar{x} \pm$ SEM, $n = 20$). These type-1 hisses averaged 0.54 s in length, in the same range as disturbance and aggressive hisses (Table 1).

Hisses of the second type, which accompanied thrusting, always occurred in a train with interhiss intervals of less than 1 s. Typically, such a series began with one or more hisses of the sort just described, but as the train progressed, hisses became increasingly 'trilled' (a rapid fluctuation in amplitude envelope). The last few hisses of a train were always trilled, and the intervals between hisses tended to be shorter toward the end of a train; such a hiss train recorded during thrusting is shown in Fig. 4c. Both classes of courtship hisses were of much lower amplitude than disturbance hisses (Table 1).

Copulatory Hissing. During some copulations, adult males emitted hisses at intervals of 4–20 s. This was seen in about 40% of the observed copulations. Copulatory hisses were of low amplitude and short duration (Fig. 4d and Table 1); they were significantly shorter than the other categories of hisses ($P < 0.001$).

Effects of Muting and Playback

Both muting, which eliminated male hissing from courtship, and playback, which provided recorded hissing during some parts of courtship, had a significant effect on the outcome of courtship. We used several numerical criteria to detect any changes in behavior which might be due to the lack of hissing. For each male, we noted attempts to court, as indicated by posturing – the first act on the part of the male that unambiguously signals courtship; the latency to first posturing and to first thrusting was also noted. We counted the number of discrete thrusting episodes during the 15-min observation period; each episode constitutes an attempt to copulate. We reasoned that a comparison of mute with normal and sham males by these measures should provide a rough

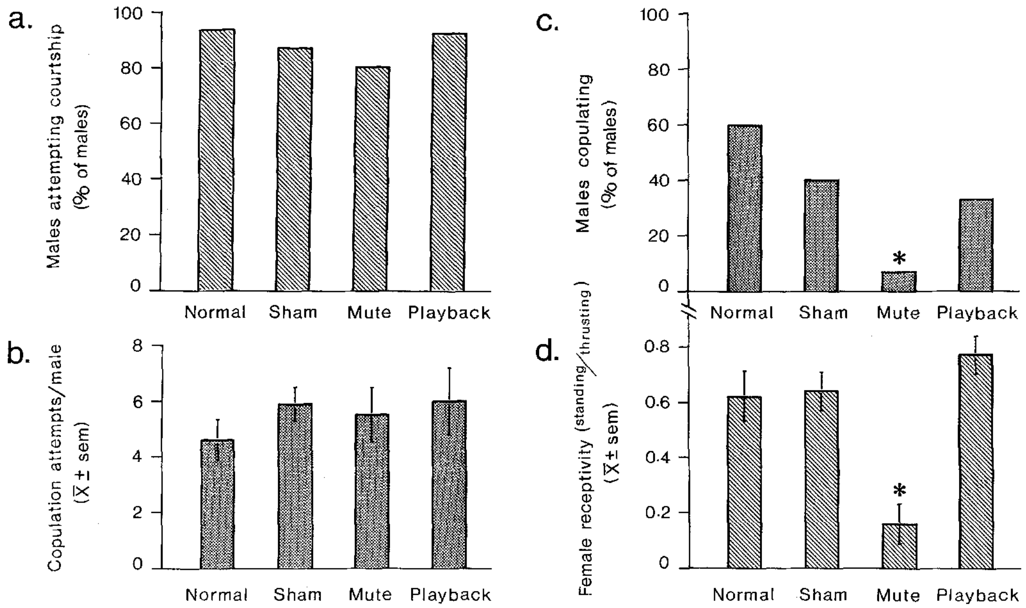

Fig. 8a–d. Comparison of the courtship behavior shown by animals in the following groups: *normal* (untreated), *sham* (sham-operated), *mute* (mute animals not receiving playback), and *playback* (mute animals receiving playback) ($n = 15$ in each group). *Asterisks* indicate significant differences. **a** Percent of males in each group that attempted to court, as indicated by posturing. No significant differences were seen among groups. **b** Mean number of copulation attempts per courting male in each group; *bars* indicate one standard error above and below the mean. No significant differences were seen among groups. **c** Percent of males successfully copulating in each group. Males in the mute group had a significantly lower success rate than all other groups ($P < 0.02$). No significant differences were found among the other groups. **d** Mean receptivity scores for females courted by males in each group. Receptivity scores were obtained by dividing the number of standing (receptive) responses by the number of thrusting episodes for each observation period. Females in the mute group had significantly lower receptivity scores than females in any other group ($P < < 0.001$). No significant differences were found among the other groups

estimate both of the normalcy of male behavior per se, and of male-female interactions, during the first stages of courtship.

We also counted the number of times that females responded to the male's thrusting by 'standing,' and established a receptivity score based on the ratio of standing to thrusting, where perfect receptivity would yield a score of 1.0, and total nonreceptivity would yield a score of 0. Finally, we counted the number of copulations achieved in each group of males. This requires specific patterns of behavior from both males and females, and represents our ultimate test for the adequacy of the male's courtship behavior.

By these criteria, the behavior of mute males appeared normal in most respects in the early phases of courtship (Fig. 8a and b). Males in all groups initiated courtship with similar frequency, and performed about the same number of copulations per observation period. There were no significant differences among groups by these measures. When we considered the timing of events during courtship, however, a significant difference emerged between those groups in which males were unable to hiss in the early stages of courtship (mute und playback groups), and those groups in which males were hissing throughout courtship. Males in all categories began posturing with similar latencies (2.34 ± 0.58 min in mute and playback groups, vs 2.57 ± 0.74 min in the normal and sham groups; ±SEM), but males in the silent groups spent significantly more time in the early phase of courtship (antennation and posturing) before making their first attempt to copulate. Mean time to first copulation attempt was 8.72 ± 1.07 min for the silent groups, compared to 5.28 ± 0.75 min for the hissing groups ($\bar{x} \pm \mathrm{SEM}$; $P < 0.01$).

In the last stages of courtship, after thrusting and therefore sound playback had begun, males and females in the mute group showed significant differences from all other groups, including the playback group. Females paired with mute males had a much lower receptivity score than any other group of females, and mute males, with a single exception, failed to copulate (Fig. 8c and d).

In contrast, neither males nor females of the playback group differed significantly from sham or normal animals in these respects. Females hearing a playback signal during the male's thrusting had receptivity scores well within the normal range, and mute males receiving playback therapy achieved near-normal rates of copulation (Fig. 8c and d).

Discussion

Does *Gromphadorhina portentosa* communicate by sound? Evidence for concluding that it does is provided by the fact that distinctly different sounds are produced in different contexts, and by the fact that both blocking the production of sound, and restoring sound artificially, have significant effects on social behavior.

The first evidence for sound communication was derived from an analysis of the context of sound production: both the range of settings in which hissing occurred, and the specificity with which hissing was linked to other stereotyped behaviors. In *G. portentosa,* sound production was closely associated with three social contexts: courtship, copulation, and territorial defense, in addition to its association with disruptive stimuli. In two social situations hissing accompanied specific stereotyped behaviors with high frequency: posturing and thrusting during courtship, and abdomen-thrashing during aggressive interactions. These ritualized behaviors figure largely in social interactions.

Further evidence was derived from analysis of the acoustical differences among hisses emitted in different contexts. A correlation between a specific change in the sound and a change in context not only would suggest that communication by sound exists, but should give some indication of the variables that might convey information. In *G. portentosa* there are reliable differences among the hisses produced in different social and nonsocial contexts. These differences lie mainly in the amplitude domain; the shape of the amplitude envelope and the relative amplitude are consistently different for the different categories of hisses. The temporal patterning of interhiss intervals may also contribute to the distinctiveness of some hiss types (courtship hissing, in particular). On the basis of these features, it is possible to identify five sorts of hisses unambiguously.

Finally, strong evidence for communication by sound was derived from observations of interactions between females and mute males, with and without replacement therapy in the form of playback of recorded hisses. It is clear from the results of muting per se that some feature of hissing is important for courtship, since females acted much less receptive with mute males. It seems extremely likely that the important feature is airborne vibration, since when females were being played recorded hisses during the male's courtship they responded with normal receptive behavior, and since under the conditions of the playback experiment only the acoustical features of hissing were being reproduced. The fact that our playback signal was so effective in eliciting female receptive behavior also suggests that much of the frequency information present in the hiss may be ignored by recipients. Although actual hisses contain considerable energy well into the ultrasonic range (Fig. 3), the playback signal had essentially no energy above 16 kHz (Fig. 1). Thus it is possible (a) that *Gromphadorhina* has evolved a simple means of sound production resulting in broad-band noise, and (b) that the animals ignore much of the information present in the sound and respond primarily to the lower-frequency, higher-energy portion of the sound spectrum. Further study of the receptor system (Nelson, 1979b) and additional playback experiments should clarify this question.

Type-2 hissing by the male during the later stages of courtship appears to elicit a specific stance from the female which is necessary for copulation to occur. A similar function has been suggested for courtship stridulation in several other Orthoptera (Alexander, 1967), but in the present case we can document the link between a specific acoustical signal and a specific behavior from the recipient. Type-2 hissing was also the only hiss which had an obligatory association with a particular behavior on the part of the sender; thrusting and type-2 hissing occurred only in conjunction.

In contrast, type-1 hissing and posturing were often, but not always, linked. The less drastic changes in behavior seen in early courtship may reflect the less predictable relationship between type-1 hissing and other courtship behavior. Elimination of type-1 hissing from the male's courtship display, which occurred in both mute and playback groups, may be related to the increased time spent by males of these groups in the early stages of courtship (before thrusting begins). The usual sequence of events in courtship (posturing→contact by the female→thrusting by the male) appeared to be disrupted in these groups, in that females appeared to establish body contact less often and to remain in contact for a shorter time when courted by mute males. The idea that type-2 hissing is particularly important in courtship is reinforced by our observations of another species of *Gromphadorhina, G. chopardi.* In this species the male emits similar hisses at the same point in courtship, but there is a rigid alternation of hiss trains and brief thrusting episodes.

How has this mechanism of communication evolved? In *Gromphadorhina,* hissing may have evolved initially as an antipredator device, perhaps derived from a defensive spray apparatus as in *Diploptera* (Eisner, 1958). This hypothesis is supported by the fact that both males and females, including juveniles, have the capacity to hiss; as several authors have pointed out, this suggests an originally defensive function (Leston and Pringle, 1963; Roth and Hartman, 1967). Thus a transition may have occurred from interspecific defensive signaling during predation to intraspecific offensive signaling during territorial defense, with a subsequent development of species-specific courtship signals. In this context the species differences in temporal characteristics of disturbance hisses, reported by Roth and Hartman for four species of *Gromphadorhina* (1967), may represent a preadaptation for courtship hissing as a reproductive isolating mechanism.

Behaviors other than sound production are clearly important in courtship, and in aggressive interactions as well. Antennation always initiates both courtship and aggressive display; this suggests that either contact chemoreception or olfaction or both are involved in species and sex recognition. In both contexts male posturing occurs, with extension of the pregenital segments (at which time a strong odor becomes noticeable). Thus olfactory cues appear to be involved in these social interactions, as is the case for other Orthoptera, particularly cockroaches (e.g., Shorey, 1973). It seems clear from our observations and experiments, however, that for *Gromphadorhina* sound production plays an important role in communication, and may at one point in courtship be obligatory.

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Note Added in Proof

Preliminary work on the receptor system has been carried out and is reported in:

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