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Vibratory communication in spiders

I. Representation of male courtship signals by female vibration receptor

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Summary. 1. Both amplitude and frequency contents of male courtship vibrations of *Cupiennius salei* change with signal propagation through a bromeliad (Fig. 3). Temporal pattern and carrier frequency of the opisthosomal signal (Fig. 1a) remain largely unchanged, however, and therefore satisfy the requirements to carry species specific information. Pedipalpal signals cover a broad range of frequencies (Fig. 3a, c); both their dispersive transmission and the frequency-dependent attenuation by the plants may provide the female with information about her distance from the male.

2. Parallel processing of different signal components already begins in the female's metatarsal lyriform vibration receptor. *Opisthosomal signals:* They mainly elicit responses from long distal slits; signal amplitude is of only minor influence (Fig. 7). Carrier frequency is represented by interspike frequencies of individual slits (Fig. 8b, d). *Pedipalpal signals:* They elicit responses from all slits (Figs. 6, 7a). Responses of individual slits differ and can be assigned to specific frequency components contained in a pedipalpal signal (Figs. 6, 8a, 9b).

3. The repetition of opisthosomal signals within the male courtship vibration improves the signal to noise ratio in the female's receptor response (Fig. 10).

4. For unknown reasons the intensity of the receptor response follows changes in acceleration amplitude in the case of heterospecific but not in the case of conspecific courtship vibrations (Fig. 11).

Key words: Vibratory communication – Signal coding – Mechanoreception – Pattern recognition – Spider

Introduction

Male and female of the tropical wandering spider *Cupiennius salei* exchange vibratory signals to communicate during courtship (Barth 1986). These signals are transmitted through the leaves of monocotyledonous plants on which spiders of the genus *Cupiennius* are predominantly found (Rovner and Barth 1981; Barth et al. 1988). The males produce (i) opisthosomal signals (which are also designated as syllables) by bobbing with the opisthosoma and (ii) pedipalpal signals by scratching and drumming with the pedipalps against the substrate (Fig. 1a). These signals are species specific (Barth 1992), and it has been demonstrated that vibratory communication is an important filter mechanism serving species recognition and species isolation (Barth and Schmitt 1991). Male courtship series (Fig. 1a) of different species differ in details such as the duration of the syllable, the number of syllables in a series, the change of signal amplitude within a series of syllables, etc. (Barth 1992). Behavioural experiments have shown that opisthosomal signals are necessary and sufficient for eliciting a female response in *C. salei* (Schüch and Barth 1990). A possible function of pedipalpal signals is to inform the female about the location of the male (Schmitt et al. 1992).

To understand the neuroethology of vibratory communication in spiders it is important to know how signals change during propagation in plants and how the sense organs process the information contained in the signals. Two types of vibration sensitive sensilla are known in spiders: vibration sensitive hairs (Speck-Hergenröder and Barth 1988) and slit sensilla (Barth and Libera 1970). Among the slit sensilla the metatarsal lyriform organ (MO, a compound slit sense organ) is exceptional due to its mid-dorsal position on the metatarsus near the tarsus-metatarsus joint and the orientation of its slits perpendicular to the leg's long axis. Both these features favour the perception of tarsal movements induced by substrate vibrations. The MO is the most sensitive vibration receptor known in spiders and threshold curves of its individual slits have already been presented (Barth and

Abbreviations: *MO* metatarsal lyriform organ; *ISFH* interspike frequency histogram; *FFT* Fast Fourier transform; *PSTH* peristimulus time histogram

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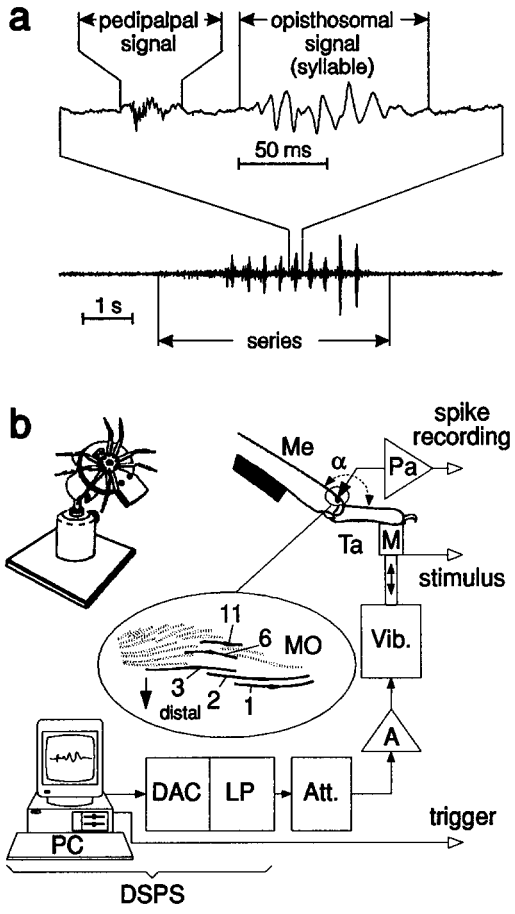


Fig. 1a, b. Structure of male courtship vibrations and experimental setup. **a** Male courtship vibrations are structured in series and consist of opisthosomal signals (syllables) and pedipalpal signals. **b** The stimulus signal obtained from the digital signal processing system (*DSPS*) drives an electrodynamic vibrator which displaces the tarsus dorsoventrally against the metatarsus. *Me* metatarsus waxed to the end of metal leg of spider dummy (inset); *Ta* tarsus freely resting on accelerometer (*M*); α angle between tarsus and metatarsus; *PC* personal computer; *DAC* digital analog converter; *LP* low pass filter (0–3.75 kHz); *Att* attenuator; *A* power amplifier; *Vib* vibrator; *Pa* preamplifier for spike recording. *MO* expanded view of metatarsal lyriform organ with slit arrangement; recordings were done from slits drawn in bold lines (long slits 1–3, 140–190 µm; short slits 6 and 11, 75–90 µm; Van de Römer 1980); numbers refer to slits quoted in text

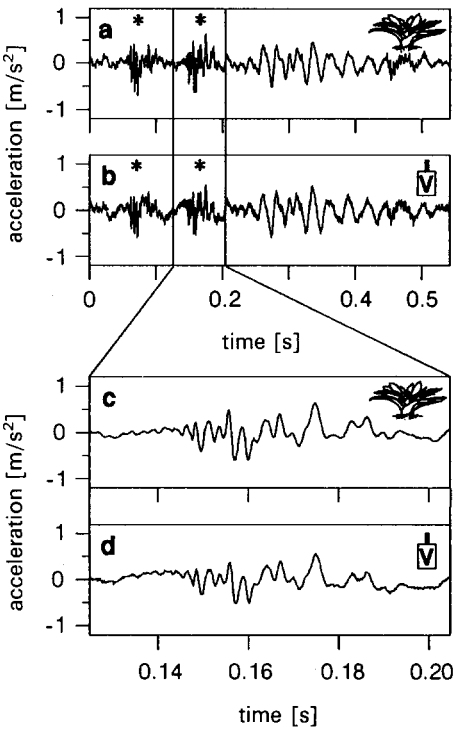


Fig. 2a–d. Original recordings and playbacks of male courtship vibrations of *Cupiennius salei*. **a** Part of a male vibration recorded on a bromeliad and consisting of two pedipalpal signals (*) followed by one syllable (opisthosomal signal). **b** Same signal as in **a**, but played back using experimental setup shown in Fig. 1b. **c, d** Expanded view of original record (**c**) and playback (**d**) of pedipalpal signal

Geethabali 1982). No marked tuning of single slits to limited frequency ranges was found.

In the present study we describe how the ensemble of slits in the female MO depicts different frequency components, amplitudes and temporal patterns of the complex male vibrations. Signal modification by transmission through the plant is taken into account by analyzing and applying vibrations recorded close to the male and at some distance from it.

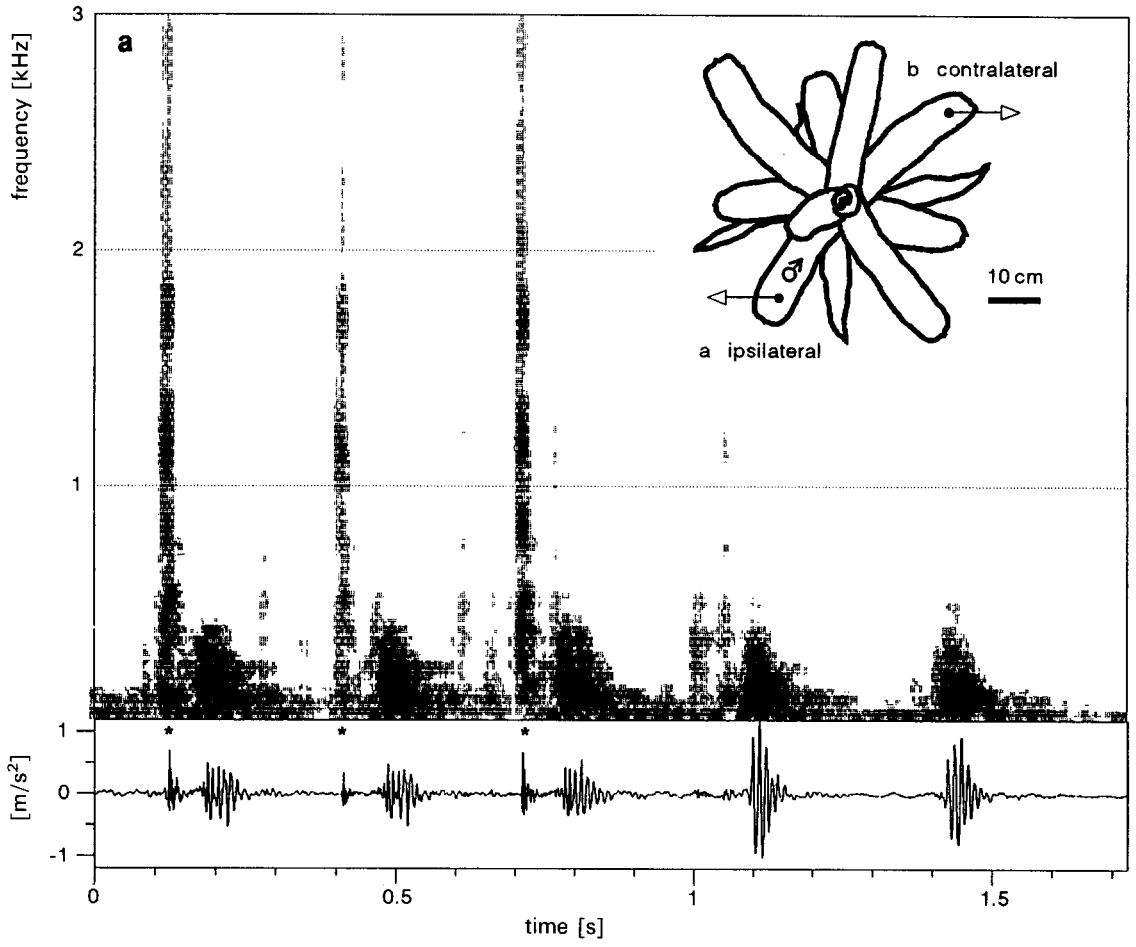
Materials and methods

Animals. All electrophysiological experiments were performed with female spiders of the species *Cupiennius salei* Keys. (Lachmuth et al. 1984). Courtship vibrations were recorded from males of *C. salei*, *C. getazi* and *C. coccineus*. All animals were adults (age 12–15 months after leaving the egg sac) and laboratory bred.

Recording and analysis of male courtship vibrations. A female and a conspecific male were allowed to move freely on a bromeliad. After courtship began, vibrations were recorded using 4 accelerometers (B&K 4375) waxed onto the mid region of 4 different leaves. Thus it was possible to record the courtship vibrations simultaneously at various locations. The output of the accelerometers was amplified (B&K 2635) and recorded with a four-channel FM tape recorder (Racal STO4DS). Vibrations recorded simultaneously on two different leaves were further analyzed using a two-channel digital signal processing system (Baurecht et al. 1989) which also served as a source of vibratory stimuli for subsequent experiments.

All frequency analyses (FFT) were performed using acceleration values of vibratory signals as the input parameter. The amplitude

Fig. 3a–d. Sonagram and oscillogram of courtship vibration of a male *Cupiennius salei*. Inset in **a** shows recording arrangement. **a, b** Oscillogram and sonagram (range shown here: 35 dB) of vibrations recorded on the ipsilateral (**a**) and contralateral leaf (**b**) relative to position of signalling male. Pedipalpal signals (*) contain high-frequency components only on the ipsilateral leaf. Note increased acceleration amplitude of the last two of 5 syllables (opisthosomal signals) only on ipsilateral (**a**) but not on contralateral leaf (**b**). **c** FFT of one pedipalpal and **d** FFT of one opisthosomal signal recorded on the ipsilateral (—) and contralateral (···) leaf. Note stronger attenuation of high-frequency components than of low-frequency components seen in the FFT of pedipalpal signal (**c**). 0 dB corresponds to the highest amplitude in **d**


a
frequency [kHz]
3
2
1
b contralateral
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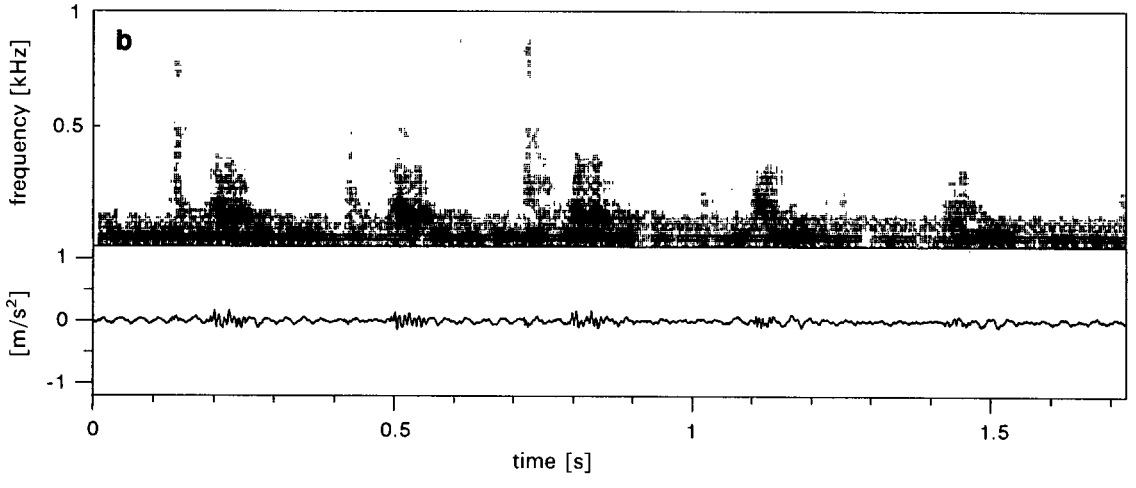
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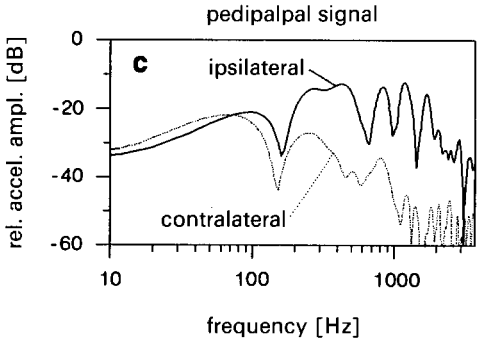
pedipalpal signal
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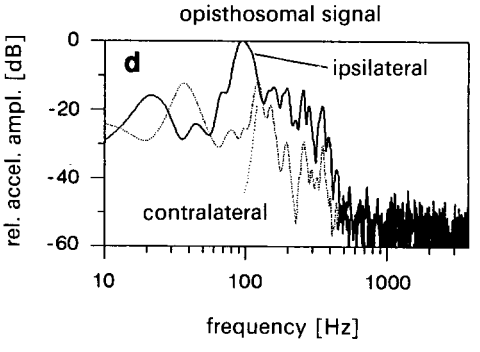
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part of the resulting frequency spectrum is referred to as the frequency contents of the signal processed.

Behavioural experiments. Previously recorded courtship series were used to determine the number of behavioural responses of females ($N=6$) to 10 identical courtship series as described by Schüch and Barth (1990). Response frequency is given as the percentage of females responding at least once (probability p) and as rate of responses (rate r; non-responding females not considered).

Stimulation in electrophysiological experiments. The animals were waxed onto a metal spider dummy (inset Fig. 1b) with a mixture of beeswax and colophonium. The dummy legs could be adjusted to the individual length and position of the spider legs. Thus a quasi-natural posture of the spider was ensured and uncontrolled strains in the exoskeleton were avoided. Zero position between tarsus and metatarsus was adjusted to 170° by optical control, an angle which is often observed in the first and second leg of females under courtship conditions.

An electrodynamic vibrator (Ling V106) was used to apply vibratory stimuli. An accelerometer attached to the tip of the moving vibrator axis measured the stimulus applied to the distal end of the tarsus (Fig. 1b). The tarsus rested freely on the accelerometer. This results in threshold curves essentially similar to those obtained with the tarsus firmly coupled to the vibrating substrate (Barth and Geethabali 1982). Regarding the acceleration amplitude, the frequency response of the vibrator was flat in the frequency range of interest (50–500 Hz, −3 dB range; 50 Hz–2 kHz, −6 dB range). Therefore, the output vibratory signal of the vibrator matches the previously recorded vibrations; this guaranteed high quality of signal reproduction (Fig. 2).

Electrophysiological and stimulus equipment were mounted on separate levelling plates which rested on sand to reduce vibratory coupling. In addition the whole setup was carried by pneumatic stabilizers to reduce background vibrations. In spite of all these precautions inevitable vibratory noise leads to a "spontaneous" spike frequency in long slits. This problem is known from earlier experiments (Barth and Bohnenberger 1978; Barth and Geethabali 1982) and is probably related to the high sensitivity of these slits.

Ten identical courtship series separated by pauses of 5 s were applied as one stimulus sequence. In the courtship of *C. salei* the pause between two consecutive male vibration series is 8 to 10 s (Schüch and Barth 1985). The most sensitive slit returns to its spontaneous discharge rate within 2 s after the end of a series (see below). This indicates that the pause duration chosen in the experiment is long enough to avoid an influence of preceding stimuli on the receptor response.

Electrophysiological recording and data evaluation. All data refer to recordings from the first two leg pairs. Electrolytically tapered tungsten electrodes were used to record action potentials extracellularly from individual receptor cells of identified slits of the MO (Fig. 1b) as previously described (Barth 1967, 1972). Receptor responses were recorded together with the stimulus signal and trigger impulses obtained from the digital signal processing system using a PCM tape recorder (Instrutech VR100). A laboratory interface (CED-1401) and computer equipment were used for data analysis.

Spike analysis and statistics. To compare the frequency contents of a vibratory stimulus with that of the spike pattern elicited by it, we calculated the corresponding interspike frequency histogram ISFH of the response. To obtain an ISFH we grouped all interspike frequencies (reciprocal values of spike intervals) which occurred during the stimulus into classes of 10 Hz bin width. Nonparametric statistics were used because data were not normally distributed (Siegel and Castellan 1988). The number of animals is referred to as N, the number of sweeps analyzed is given by the number of stimuli per slit multiplied by N. The PSTH of each slit shows the sum of responses of all tested animals.

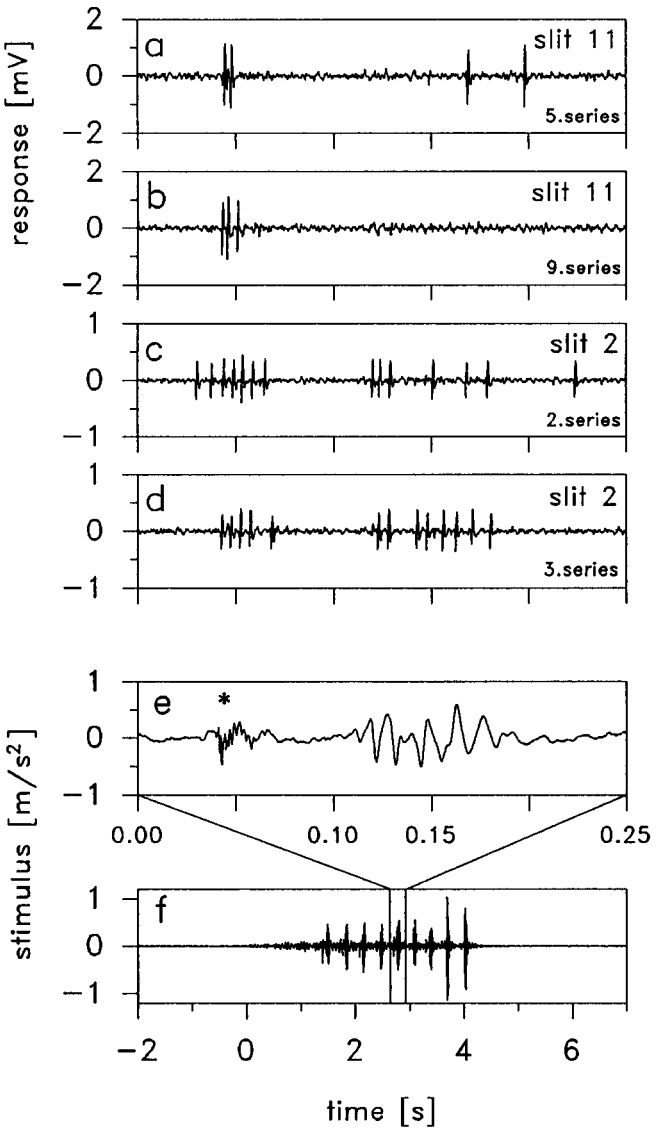


Fig. 4a–f. Responses of slit 2 and slit 11 of the MO to part of male courtship vibrations. **a, b** Typical recordings from same slit 11 show responses mainly to pedipalpal signals (*); note variability of responses to identical stimuli. **c, d** Typical recordings from slit 2 show response to both pedipalpal and opisthosomal signals; again, note variability of response. **e** Part of vibrations shown in **f**, with pedipalpal (*) and opisthosomal signal (syllable). **f** Male courtship series (duration 4.4 s) which was used as vibratory stimulus (10 identical series with 5 s pause in between)

Results

Changes in male courtship vibrations due to propagation

We analyzed typical male courtship vibrations encountered by the female at different distances from the male and later used them as stimuli in behavioural and electrophysiological experiments. Male vibrations containing pedipalpal and opisthosomal signals were recorded simultaneously (i) 10 cm away from the male on the same leaf (ipsilateral leaf) and (ii) about 50 cm away from the male on a leaf opposing the first one (contralateral leaf; inset, Fig. 3a). Our aim was to show representative

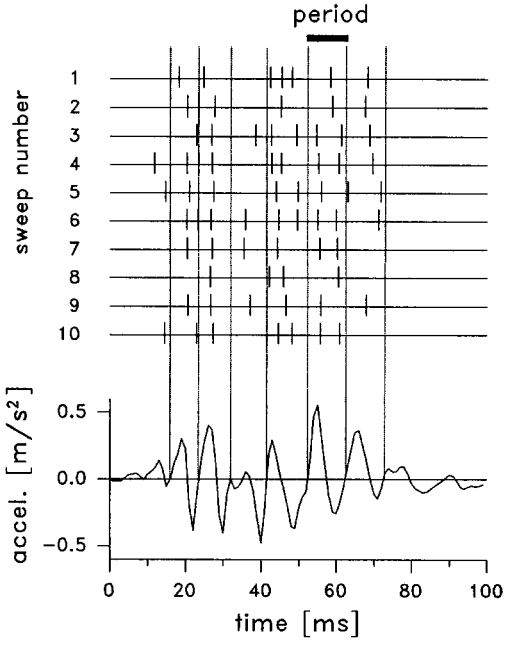


Fig. 5. Variability of response of individual slit 2. Responses to one syllable of 10 successive stimuli (for stimulus see Fig. 4f). One stimulus period (in between two neighbouring broken lines) elicits either one or two or no spikes

changes in male courtship vibrations during propagation rather than to describe details of the transmission properties of bromeliads. Attenuation properties of monocotyledonous plants are known for bananas (Barth et al. 1988) and agaves (Wirth 1984). They are irregular and frequency-dependent.

Pedipalpal signals. Drumming and scratching of the pedipalps against the leaves occurs exclusively between two opisthosomal signals (Schüch and Barth 1985). Pedipalpal signals differ from opisthosomal signals in duration and frequency contents (Fig. 3a). Physically, drumming can be regarded as a series of impacts which lead to a flat frequency spectrum near the signal source (Fig. 3c). The highest acceleration amplitude of pedipalpal signals was 0.7 m/s² (measured on the ipsilateral leaf). Frequency contents change with time in an ongoing pedipalpal signal (for a representative example see Fig. 6b). Detailed analysis of 19 single pedipalpal signals ($N=3$) measured about 10 cm away from the signalling male on the ipsilateral leaf shows high-frequency components (>1 kHz) only at the beginning of the signal; their duration[1] was 7.2±2.1 ms. Medium-frequency components (peak frequency between 250–550 Hz) also occur at the beginning of the pedipalpal signal, but show a longer duration of 14.2±5.2 ms. Low-frequency components (<200 Hz) are present before, during and after the pedipalpal signal.

Attenuation of signals transmitted to the contralateral leaf increases with increasing frequency. High-frequency components (>1000 Hz) are attenuated by more than

[1] Duration: time period within which corresponding frequency components are attenuated by 10 dB

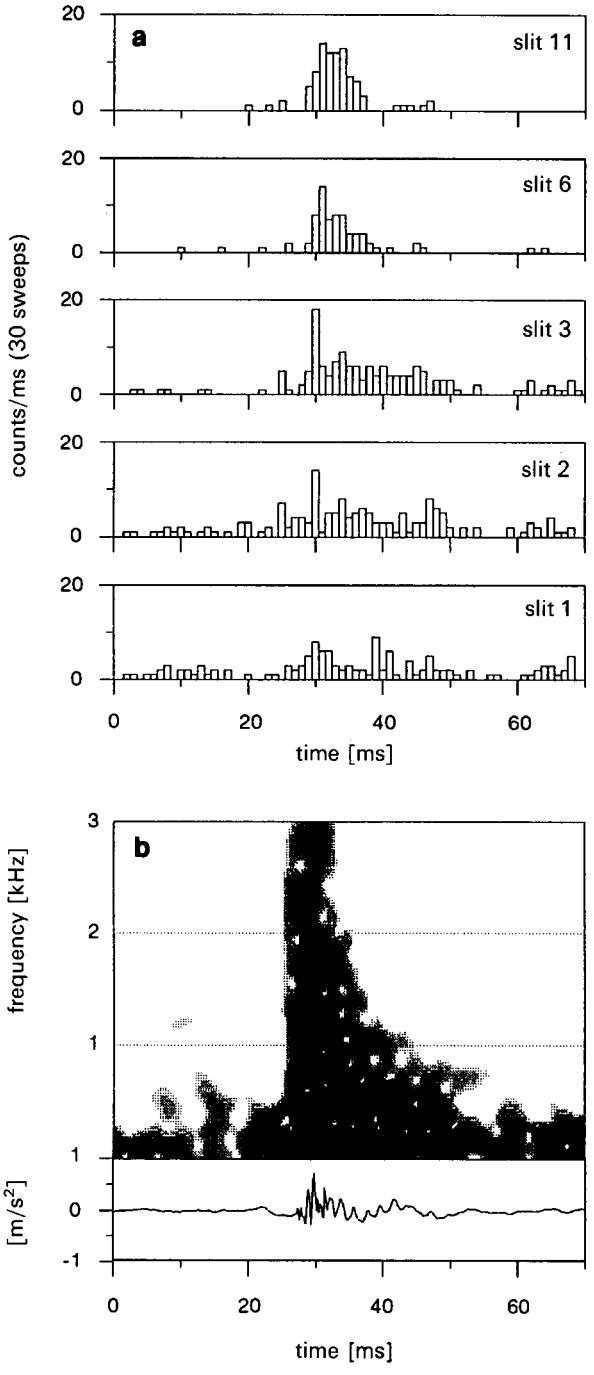


Fig. 6a, b. Frequency contents of pedipalpal signal and PSTH of the responses in different slits (each slit tested in 3 animals, 10 sweeps per slit). **a** Duration of response of short slits (6 and 11) roughly corresponds to duration of high-frequency components of stimulus; duration of response of long slits (1–3) corresponds with that of low-frequency (slit 1) and medium-frequency components (slit 3) of stimulus. **b** Oscillogram and sonagram of a pedipalpal signal (part of stimulus shown in Fig. 4f). Sonagram (range shown here: 35 dB) shows typical frequency contents of a pedipalpal signal recorded 10 cm away from the male

30 dB and are therefore nearly nonexistent on the contralateral leaf. Medium-frequency components (250–550 Hz) are attenuated by 15–30 dB and only partially represented on the contralateral leaf, whereas low-frequency components (<200 Hz) are attenuated even less and

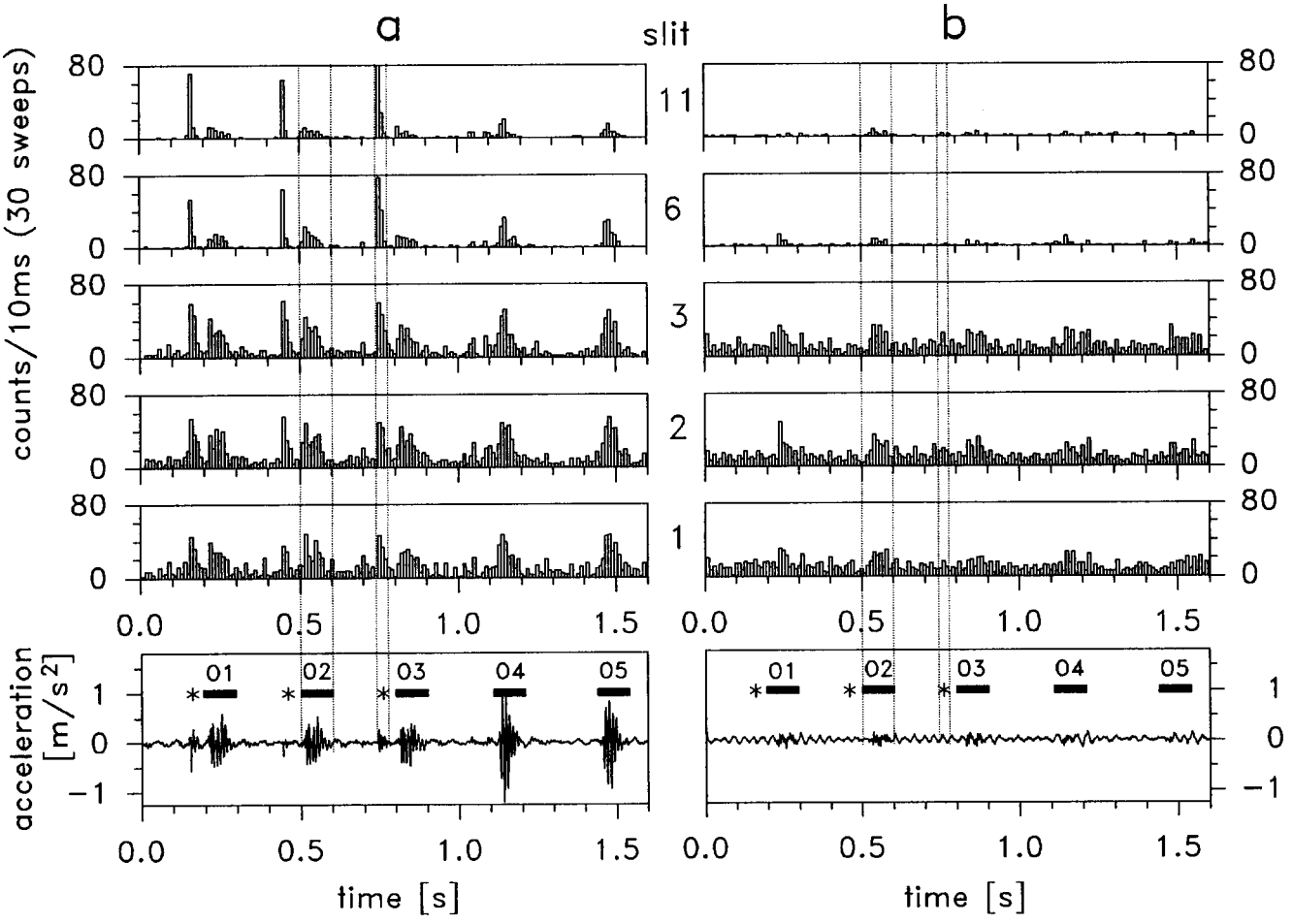
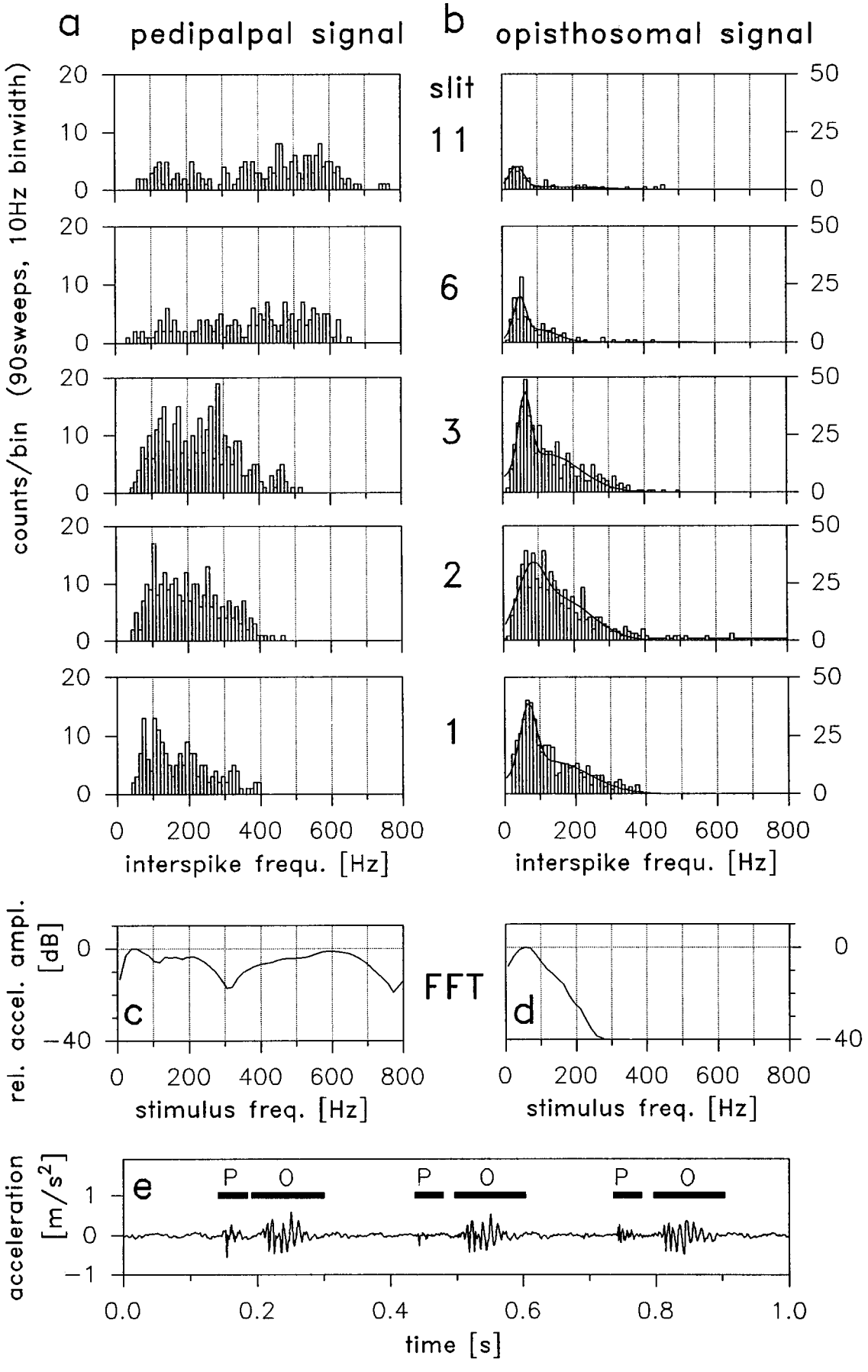


Fig. 7a, b. PSTH of the response of different slits of the MO to male vibrations containing pedipalpal and opisthosomal signals (each slit tested in 3 animals, 10 sweeps per slit). **a** Response to vibrations recorded on the ipsilateral leaf only 10 cm away from the signalling male. All slits respond to pedipalpal signals (*). Opisthosomal signals (*O1–O5*) preferentially stimulate long distal slits (1–3). **b** Response (same slits) to vibration as in **a** but modified after having travelled to the contralateral leaf. Due to strong attenuation of high-frequency components of pedipalpal signals (Fig. 3) virtually no response is seen in short slits 6 and 11. In contrast, opisthosomal signals *O1–O5*, despite their attenuation, elicit substantial responses in long slits 1–3. Time periods marked by bars refer to analysis described in the text

are therefore well represented on the contralateral leaf ($N=1$, $n=7$; for a representative example see Fig. 3a–c).

Opisthosomal signal. The highest acceleration amplitude of syllables was 1.1 m/s² (recorded on the ipsilateral leaf). The waveform of the signal can be approximated to an amplitude-modulated sine wave (Fig. 1a) whose carrier frequency varies between 60–100 Hz (Schüch and Barth 1985). The attenuation of syllables propagated to the contralateral leaf changed within the same courtship series depending on the initial amplitude of the syllable. Within a single courtship series a comparison of syllables with nearly the same frequency contents (main peak frequencies differ only ± 5 Hz) revealed an attenuation by 11 dB for syllables with initial acceleration amplitudes lower than 500 mm/s² (syllables 1–3 in Fig. 3a, b) and an attenuation by 23 dB for syllables with initial acceleration amplitudes higher than 900 mm/s² (syllables 4 and 5 in Fig. 3a, b). This leads to a reversal in the amplitude pattern of consecutive syllables. The amplitudes of the last two syllables, which are the highest on the ipsilateral leaf, are the lowest on the contralateral leaf (oscillogram Fig. 3a). This result reflects the complexity of the attenuation properties of plants, although it is not a general rule. No obvious differences in syllable duration were found in vibrations recorded simultaneously on different leaves (Fig. 3a, b).

Fig. 8a–e. Distribution of spike frequencies elicited by 3 pedipalpal and 3 opisthosomal signals in different slits of the MO (each slit tested in 3 animals, 10 sweeps per slit and signal). **a** Interspike frequency distribution calculated from the response to the 3 pedipalpal signals shown in **e**. High-frequency components of the stimulus (**c**) elicit high interspike frequencies only in short slits (6 and 11). **b** Interspike frequency distribution calculated from the response to the 3 syllables (opisthosomal signals) shown in **e**. Curve fits were calculated using a double-peak distribution with maxima at the single and doubled carrier frequency of stimulus. **c** Averaged FFT of the 3 pedipalpal (*P*) and **d** of opisthosomal signals (*O*) marked in **e**. **e** Oscillogram of part of male courtship vibrations (Fig. 4f) containing pedipalpal (*P*) and opisthosomal signals (*O*). Bars show time periods of stimuli processed (*P*, 35 ms; *O*, 100 ms)


a
pedipalpal signal
b
opisthosomal signal
slit
11
6
3
2
1
counts/bin (90sweeps, 10Hz binwidth)
20
10
0
50
25
0
200
400
600
800
interspike frequ. [Hz]
rel. accel. ampl. [dB]
c
d
FFT
−40
stimulus freq. [Hz]
acceleration [m/s²]
e
P
O
1
−1
0.0
0.2
0.4
0.6
0.8
1.0
time [s]

There is a remarkable shift of the main peak frequency (representing the carrier frequency) in frequency analysis of the same opisthosomal signals measured on different leaves. In the above example the main peak frequency at 100 Hz on the ipsilateral leaf moves to 120 Hz on the contralateral leaf (Fig. 3d). Analyses of other opisthosomal signals recorded simultaneously on different leaves revealed differences of up to 20 Hz between main peak frequencies.

Behavioural response of females. The male vibrations described above and later used as stimuli in electrophysiological experiments were also tested for their behavioural efficiency in playback experiments. All females ($N=6$) responded to the male vibrations recorded on the ipsilateral leaf (probability $p=100\%$) with a rate of response $r=92\%$. There was also a behavioural response to the vibrations recorded on the contralateral leaf, yet it was reduced with regard to both the response probability ($p=33\%$) and the rate of response ($r=65\%$).

Receptor response to conspecific courtship vibrations

Recordings from slit 2 and slit 11 of the MO (Fig. 1b) show that the time of spike occurrence and the number of spikes vary when identical stimuli are presented repeatedly (Fig. 4). Long slits respond to syllables with either one or two spikes per stimulus period (Fig. 5). There are also some periods within a syllable which occasionally do not elicit a response at all. The variability of the receptor response of different animals is in the same range as that shown for an individual slit.

Temporal pattern and intensity of response

Pedipalpal signals. Detailed analysis of a single pedipalpal signal measured about 10 cm away from the signalling male on the ipsilateral leaf shows that the frequency spectrum changes during the course of the pedipalpal signal (Fig. 6b). All slits of the MO tested responded to pedipalpal signals (Figs. 6, 7a). The time course of the responses differs in individual slits, however (Fig. 6a). Long slit 1 responds when low frequencies (<200 Hz) occur in the stimulus. Therefore slit 1 responds not only during the pedipalpal signal but also before and after the end of the pedipalpal signal when low frequencies occur in the courtship vibrations. Long slit 3 responds during the duration of the pedipalpal signal when medium-frequency components (250–550 Hz) occur. Short slits (6 and 11), however, are only stimulated at the beginning of a pedipalpal signal when, in addition, high frequencies occur (Fig. 6a, see also original recordings in Fig. 4). Having travelled to the contralateral leaf, high-frequency components of pedipalpal signals are strongly attenuated (Fig. 3c). Such filtered pedipalpal signals do not elicit a response from short slits (Fig. 7b).

Opisthosomal signals. Syllables preferentially stimulate the long slits 1, 2 and 3 (Fig. 7a). The absolute number of spikes occurring during syllables does not follow the increase of acceleration amplitude typical of the last syllables in male courtship vibrations recorded on the ipsilateral leaf (for a description of male courtship vibrations see Schüch and Barth 1985). The 120% increase of the highest acceleration amplitude measured in the last two syllables of the stimulus shown in Fig. 7a leads only to a 10% increase in the number of spikes per syllable (slits 1–3, $N=3$). In comparing the highest acceleration amplitudes measured simultaneously on the ipsilateral and on the contralateral leaf, we found an attenuation of 72% (equivalent to −11 dB) in syllables 1–3 (Fig. 7) and 93% (equivalent to −23 dB) in syllables 4 and 5. Despite this strong attenuation, the number of spikes per syllable is only reduced by 19% (syllables 1–3) and 35% (syllables 4 and 5).

Frequency contents of responses

Pedipalpal signals. Responses of different slits to pedipalpal signals also differ with regard to interspike frequencies. A comparison of different slits shows a shift from low interspike frequencies in long slits (1–3) to high interspike frequencies in short slits (6 and 11; Fig. 8a). High interspike frequencies of short slits only occur when the stimulus contains high-frequency components (Fig. 8a, b). Different frequency components of the stimulus are therefore not only represented by the response of different slits but in addition elicit correspondingly different interspike frequencies in these slits.

Opisthosomal signals. Interspike frequencies elicited by syllables show a positively skewed distribution. In all slits the main peak frequency in the ISFH of the response (Fig. 8b) corresponds to the main peak frequency in the FFT of the stimulus (Fig. 8d) and thus to the carrier frequency of the syllable. The higher interspike frequencies mainly represent the first harmonic of the carrier frequency and result from two spike responses to periods contained in a syllable (Fig. 5).

Discrimination of pedipalpal and opisthosomal signals

Pedipalpal and opisthosomal signals differ with regard to their role in behaviour (Schüch and Barth 1990). A possible basis of their sensory discrimination are different spike patterns elicited in the ensemble of slits composing the MO. The Page test for ordered alternatives was used to verify whether the interspike frequencies and/or the number of spikes per tested signal are ordered by the spatial arrangement of slits in the MO (given by the slit number).

Pedipalpal signals. Whereas the median number of spikes elicited by pedipalpal signals is not ordered by slit number (3–5 spikes/pedipalpal signal; Page test, n.s.; Fig. 9a), the median interspike frequency of the responses increases significantly from distal slits to proximal slits (170–460 Hz; Page test, $p<0.001$; Fig. 9b).

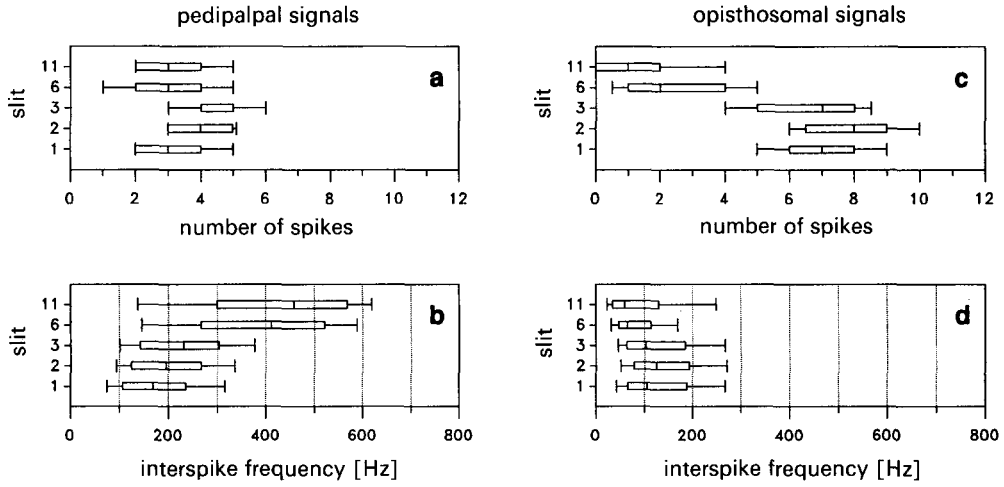


Fig. 9a–d. Comparison of spike number and interspike frequencies in responses of different slits of the MO to 3 pedipalpal and 3 opisthosomal signals (each slit tested in 3 animals, signals shown in Fig. 8). Box plots display median, tenth and ninetieth (bars) and twenty-fifth and seventy-fifth percentiles (boxes). **a** The median number of spikes elicited by pedipalpal signals is not ordered according to the spatial arrangement of slits in the MO (for relative slit position see Fig. 1b). **b** The median interspike frequency elicited by pedipalpal signals increases significantly from slit 1 to slit 11. **c** The median number of spikes elicited by opisthosomal signals decreases significantly from slit 1 to slit 11. **d** The median interspike frequency elicited by opisthosomal signals decreases significantly from slit 1 to slit 11 (in short slits 6 and 11 the calculated interspike frequency results from a few spikes only; for statistical significance see text)

Opisthosomal signals. In contrast to the effect of pedipalpal signals, the median number of spikes elicited by syllables decreases significantly from distal slits to proximal slits (1–8 spikes/syllable; Page test, $p<0.001$; Fig. 9c). Likewise, the median interspike frequency decreases significantly from distal to proximal slits (58–120 Hz; Page test, $p<0.001$; Fig. 9d).

Influence of the temporal pattern of courtship series

The above results demonstrate the importance of long slits in the representation of opisthosomal signals. The PSTH of the response of slit 2 shows a decrease of spike discharge between syllables which is typical of the response of long slits to a complete courtship series (Fig. 10). This leads to an improved signal to noise ratio, which, in addition, increases with the number of syllables. After the end of a series, the spontaneous spike frequency is reduced. In the given example (Fig. 10) it returns to its initial value within 2 s. Since the acceleration amplitudes of the opisthosomal signals used in this experiment were maximal with regard to the natural range, a duration of about 2 s of the post stimulus activity depression is considered maximal as well.

Response to courtship vibrations of different species

Behavioural response. Conspecific courtship series of two males (A, B) elicited responses in all females of *Cupiennius salei* (probability $p_A=100\%$, rate $r_A=95\%$, $p_B=100\%$, $r_B=100\%$). The same females responded less often to one tested courtship series of *C. coccineus* ($p=66\%$, $r=80\%$) and never to one of *C. getazi* (pie charts in Fig. 11). These response probabilities of female *C. salei* to the courtship series later used in electrophysiological experiments, roughly correspond to results of behavioural experiments carried out with a large number of males and females ($N>14$; *C. salei:* $p=100\%$, *C. coccineus:* $p=64\%$, *C. getazi:* $p=25\%$; Barth and Schmitt 1991).

Receptor response. Courtship vibrations of different species of *Cupiennius* mainly differ in the temporal pattern

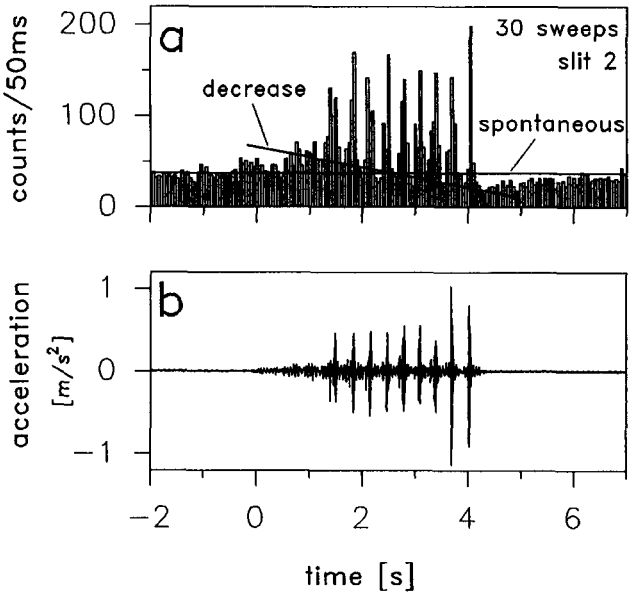


Fig. 10a, b. Response of slit 2 of the MO to one complete male courtship series consisting of 9 syllables (slit tested in 3 animals, 10 sweeps per slit). **a** PSTH of the response. Note decrease of spike frequency in between syllables in the course of stimulus series; this leads to an increased signal to noise ratio. Activity is lowered below the spontaneous level for up to 2 seconds following the end of stimulus. **b** Oscillogram of stimulus

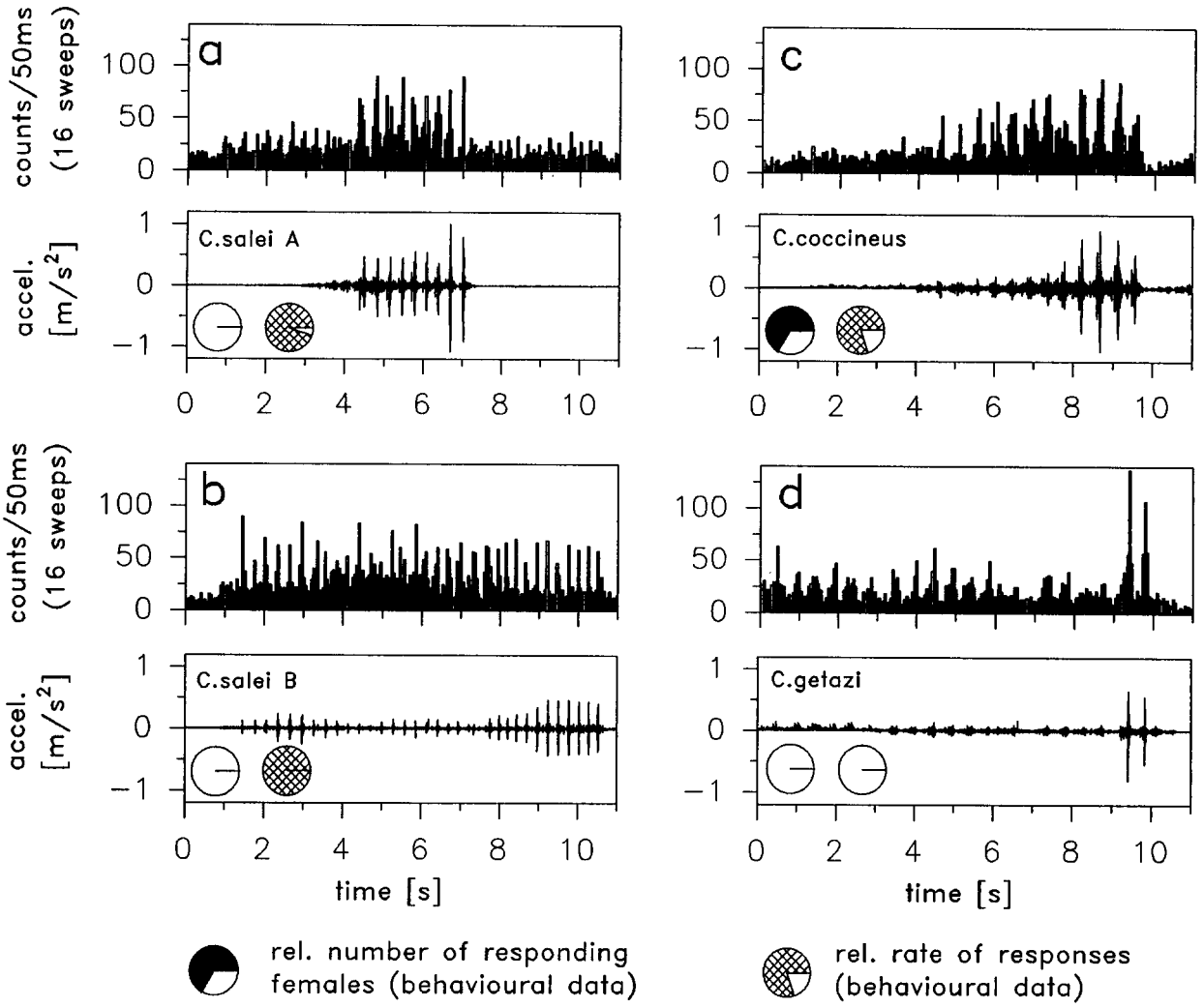


Fig. 11a–d. Behavioural and receptor response (slit 2) of female *Cupiennius salei* to male vibratory signals of different species. Pie charts show behavioural response ($N=6$). All PSTHs result from recordings from same slits and show responses to courtship vibrations of two males of *Cupiennius salei* (**a, b**), and to courtship vibrations of male *C. coccineus* (**c**) and *C. getazi* (**d**) (each courtship series tested in 2 animals, 8 sweeps per slit). Number of spikes elicited by syllables follows the acceleration amplitude only in the case of heterospecific courtship signals (**c, d**)

of opisthosomal signals (Barth 1992), which are mainly represented by the responses of long slits (see above). The PSTHs of responses of slit 2 are given as typical examples of such responses (Fig. 11). All conspecific courtship series elicit a response in which the acceleration amplitude of syllables is of only minor influence (Fig. 11a, b; see also Fig. 7a, b). Surprisingly, heterospecific series elicit responses varying with the acceleration amplitude of syllables. This is particularly evident in the response to vibrations of *C. getazi*, where the response elicited by the last two syllables with increased acceleration amplitudes is much stronger than the response to preceding syllables with low amplitudes (Fig. 11d). The intensity of response to vibrations of *C. coccineus* follows the increase of syllable amplitude (Fig. 11c).

Discussion

The use of vibratory signals for communication during courtship is widespread in arthropods (Markl 1969). In spiders, vibratory signals are of outstanding behavioural significance (Barth 1982; Uetz and Stratton 1982) and vibratory communication is known for almost every group (Robinson 1982). For spiders of the genus *Cupiennius*, vibratory communication is an important filter mechanism serving species recognition and species isolation (Barth and Schmitt 1991).

As shown by the present study the response of the vibration sensitive receptor (MO) of female *C. salei* reflects details of the temporal and spectral properties of male courtship vibrations. Pedipalpal signals cover a broad range of frequencies suited to provide information about the distance to the signal source. This information is indeed contained in the response of the female vibration receptor as discussed below.

Signal components for species recognition

Opisthosomal signals are both necessary and sufficient to elicit a female response (Schüch and Barth 1990). They

are therefore regarded as the crucial component in the male vibrations because they apparently carry the information necessary for species recognition. This information must not get lost during propagation through the plant, even over large distances. Our behavioural experiments show that females do respond to vibrations recorded at a large distance from the male (contralateral leaf); reciprocal signalling has been shown to occur between individuals that are up to 1 m apart (Rovner and Barth 1981). Only the long slits (1–3) of the MO respond to both syllables of low and of high amplitude. They are therefore considered to be responsible for coding the information contained in opisthosomal signals.

Temporal pattern of opisthosomal signals. The propagation velocity of vibrations, which is frequency-dependent in plants (Michelsen et al. 1982; Wirth 1984; Barth 1986), is about the same for all syllables due to the negligible variation in their frequency contents. Thus the temporal pattern of consecutive syllables is preserved during propagation. Temporal parameters such as syllable duration, pause duration and repetition rate were among the most influential parameters tested in behavioural experiments carried out to characterize the female releasing mechanism (Schüch and Barth 1990). At the receptor level, all these parameters are well represented by the spike trains of long slits (Fig. 7). These slits, however, also respond to pedipalpal signals; these responses are characterized by interspike frequencies similar to those elicited by opisthosomal signals (Figs. 8, 9). Interneurons may be able to represent the temporal pattern of opisthosomal signals separately by combining excitatory input from long slits (responding to both pedipalpal and opisthosomal signals) with inhibitory input from short slits (responding only to pedipalpal signals).

At least 3 syllables in a series are necessary to induce a female to respond to more than 50% of all playback series in behavioural experiments (Schüch and Barth 1990). We now know that the signal to noise ratio of the receptor response increases with increasing syllable number (Fig. 10); this may help to explain the behavioural findings.

Frequency contents of opisthosomal signals. In frequency analyses of the same opisthosomal signals measured simultaneously at various positions on the bromeliad we found differences in the main peak frequency (representing the carrier frequency of syllables) of up to 20 Hz (Fig. 3d). Although the carrier frequency of syllables is an important parameter in experiments testing the behavioural response of females, the effective range[2] eliciting a female response is large enough (60–200 Hz; Schüch and Barth 1990) to accommodate a frequency shift of 20 Hz. The frequency contents of opisthosomal signals (Fig. 8d) is well represented by the interspike frequencies elicited in the long slits of the vibration receptor (Fig. 8b).

Amplitude of opisthosomal signals. The attenuation of vibrations does not increase monotonically with distance in plants (Michelsen et al. 1982; Wirth 1984; Barth et al. 1988). In addition we found that the attenuation of single syllables may depend on their initial value, possibly indicating that only a limited range of amplitudes is transmitted by plants. We conclude that neither the absolute value nor the modulation of syllable amplitude nor the amplitude pattern of subsequent syllables within a courtship series contain essential information, because such information is potentially lost during propagation in the plant. This conjecture is supported by behavioural experiments in which *C. salei* females responded to a very wide range of acceleration amplitudes of synthetic signals (8–8000 mm/s^2; effective range, see footnote 2) and in which both the shape of syllables and the change of syllable amplitude within a series did not influence the response probability (Schüch and Barth 1990). Similarly, the receptor response to syllables of conspecific male vibrations is remarkably independent of acceleration amplitude (Figs. 7, 11). Inevitable variations of syllable amplitude are to a large extent compensated for by receptor properties. The temporal patterns of heterospecific male courtship vibrations of *C. getazi* and *C. coccineus* are represented in the activity of long slits of the MO of *C. salei* (Fig. 11). Unlike the responses to conspecific male signals (Fig. 11a, b), those to heterospecific courtship vibrations depend on the acceleration amplitudes of syllables (Fig. 11c, d). We have to assume that differences in the temporal or spectral structure of the male courtship vibrations are responsible for this surprising finding. A detailed study of the effects of temporal and spectral parameters using synthetic male vibrations is underway (Baurecht and Barth, in prep.).

Pedipalpal signals

Pedipalpal signals are not necessary for eliciting a female response (Schüch and Barth 1990). Their role in communication is not yet clear. A dispersive transmission channel like a plant might provide the receiver with information about the distance to the signal source (Michelsen et al. 1982; Keuper and Kühne 1983) if (i) the signal contains several frequency components propagated with different velocities in a dispersive medium, if (ii) the receiver is able to perform a rough frequency analysis and if (iii) the CNS is able to process the temporal pattern of the different frequency components.

Pedipalpal signals and receptor properties satisfy the first two requirements. (i) Pedipalpal signals cover a broad range of frequencies (Fig. 3c). (ii) The MO performs the required frequency analysis by separating the frequency contents of the stimulus into different frequency components which elicit responses from different slits (Fig. 6). Regarding condition (iii), no experimental data are available at present, but the CNS may well be able to provide this capacity.

Frequency-dependent attenuation may provide the female with still another clue to judge her distance from the signalling male. High-frequency components of pedipalpal signals are attenuated more than low-

[2] Effective range: range of values within which at least one animal responds to more than 50% of the tests (Schüch and Barth 1990)

frequency components on their way through the plant (Fig. 3c). The highest detectable frequency of a pedipalpal signal therefore is a measure for distance to the signalling male. The sensory capabilities of the MO would clearly allow for such a possibility.

Distances from any vibration source emitting several frequencies (such as vibrations produced by prey) could be determined in the same two ways. Behavioural data on distance determination are only available for several species of semi-aquatic spiders (genus *Dolomedes*, Bleckmann 1991). The propagation of water surface waves is both dispersive and frequency-dependent with regard to attenuation (similar to propagation of vibrations in plants). *Dolomedes* mainly uses the curvature of the wave front to determine the distance to the signal source (Bleckmann 1991). A similar mechanism of distance orientation seems to be highly unlikely on plants, however, because of the complex structure of their surface.

Threshold values and transfer characteristics versus response to complex signals

Threshold curves of spider vibration receptors show no tuning to a limited frequency range (leg nerve recordings of *Tegenaria* and *Zygiella*, Liesenfeld 1961; pretarsal slit of *C. salei*, Speck and Barth 1982; MO of *Dolomedes triton*, Bleckmann and Barth 1984; MO of *C. salei*, Barth and Geethabali 1982). Despite the overall similarity of the threshold curves of the various slits of the MO of female *C. salei*, there are differences of threshold values as large as 1.5 orders of magnitude at certain frequencies (Barth and Geethabali 1982). These differences cannot explain our findings (measured under identical conditions: dorsoventral displacement, loose coupling of tarsus and vibrator). In contrast to the earlier finding that thresholds (sinusoidal stimulation) of slit 6 are lower than those of slit 1 for all frequencies higher than 40 Hz (Fig. 6a in Barth and Geethabali 1982) we found that the response elicited by opisthosomal signals (natural stimuli, carrier frequency about 100 Hz) is stronger in slit 1 than in slit 6 (Fig. 7a, b).

In addition to threshold curves, transfer characteristics are used to describe receptor properties. Calculations based on the transfer function fully describe the response properties in the linear range of the receptor. The slit system of another compound slit sense organ of *C. salei* was found to be linear only at frequencies below 4–8 Hz (Bohnenberger 1981). This frequency is high enough to allow the prediction of responses to stimuli connected with a proprioceptive function but too small to predict the response to courtship signals. In the nonlinear range of a receptor the response to a single-frequency component embedded in a complex stimulus could well differ from the response to a single-frequency stimulus. Behavioural experiments with *C. salei* (Hergenröder and Barth 1983) and electrophysiological recordings both from the MO (Barth 1985) and from the CNS of *C. salei* (Speck-Hergenröder and Barth 1987) have indeed shown that using band-limited noise instead of sine wave stimuli lowers threshold values considerably.

Threshold curves and transfer functions are no sufficient basis for fully understanding the response in the nonlinear range of a receptor. Our analysis underlines the importance of applying behaviourally adequate stimuli if we want to correlate behavioural with neurophysiological data.

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