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Seismic signal production in a wolf spider: parallel *versus* serial multi-component signals

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Summary

Animal signals can consist of multiple parts within or across sensory modalities (multi-component signals or multimodal signals). While recent work has focused on multimodal signals, the production, processing and evolution of multi-component signals has received considerably less attention. Here, using synchronous high-speed video and laser vibrometer recordings followed by experimental manipulations of putative sound-producing structures, we explored the mechanisms of seismic signal production in the courtship display of *Schizocosa stridulans* Stratton. Two types of seismic courtship signals were observed: 'rev' and 'idle' signals. Revs consist of a high-frequency component produced by flexions of the male pedipalp (stridulation) simultaneous with a low-frequency component produced by movements of the abdomen (tremulation). This multi-component signal is produced by independent structures and represents a parallel multi-component display. By contrast, idle displays consist of a high-intensity component produced by drumming of the forelegs on the substrate (percussion) followed by a high-frequency component produced by flexions of the male pedipalp (stridulation). While the components of the idle display are also produced by independent structures, the leg drumming and palp flexions occur serially and do not overlap in time. We discuss the selective pressures that may drive the evolution of multiple sound-producing structures as well as the selective pressures that drive the evolution of parallel *versus* serial multi-component signals.

Key words: seismic signal, courtship display, *Schizocosa stridulans*, signal evolution, multiple signal, vibratory display.

Introduction

Multiple signals (Hebets and Papaj, 2005) are common in animal communication and there has been a recent rise in studies examining the evolution and processing of multiple signals (Candolin, 2003; Hebets and Papaj, 2005; Iwasa and Pomiankowski, 1994; Johnstone, 1996; Moller and Pomiankowski, 1993; Partan and Marler, 1999; Partan and Marler, 2005; Pomiankowski and Iwasa, 1993; Rowe, 1999; Uetz and Roberts, 2002). One category of multiple signals is multi-component signals – those characterized as having multiple parts within a single sensory modality (Candolin, 2003; Hebets and Papaj, 2005; Rowe, 1999). For example, many song birds include a diversity of distinct syllables in their songs (Catchpole and Slater, 1995), and the seismic songs of some jumping spiders feature three distinct components (Elias et al., 2003). While the evolution and function of complex signaling has been the focus of a growing body of work, there are currently few studies examining the mechanisms underlying the production of multiple signals.

Acoustic multi-component signals can be produced using the same or independent structures. Most work on multi-component song production has been conducted in song birds and frogs, which, like many vertebrates, produce songs using complex air expulsion apparatuses (Gerhardt and Huber, 2002; Goller and Suthers, 1995; Suthers, 1990; Suthers et al., 2004; Suthers and Zollinger, 2004). Studies of sound production in vertebrates tends to be focused on a small number of structures and locations (e.g. syrinx in birds, vocal folds in frogs) although there are some notable exceptions: for example, manikins (Bostwick and Prum, 2005) and some fish (Ladich, 2000; Ladich and Bass, 1998). By contrast, acoustic signal production in arthropods is not limited to specific structures and song-producing devices and can be found on virtually any part of their hard exoskeleton (Dumortier, 1963; Ewing, 1989; Legendre, 1963). In addition, arthropods can produce acoustic/vibratory signals using a myriad of mechanisms (air expulsion, percussion, vibration/tremulation, stridulation, tymbal, and 'stick-and-slip' mechanisms), each of which can be found anywhere on their body (Dumortier, 1963; Ewing, 1989; Gerhardt and Huber, 2002; Huber et al., 1989; Legendre, 1963; Markl, 1983; Patek, 2001; Rovner, 1980; Uetz and Stratton, 1982). Although many arthropods can produce multi-component songs with different mechanisms as well as different structures (Cokl and Doberlet, 2003; Cokl et al., 2004; Gogala, 1985; Kalmring, 1985; Kalmring, 1997; Moraes et al., 2005; Popper et al., 2001; Virant-Doberlet and Cokl, 2004), most work on sound-production mechanisms in arthropods has focused on relatively simple calling signals of acoustic Orthoptera (Bailey and Rentz, 1990; Gerhardt and Huber, 2002; Huber et al., 1989; but see Kalmring, 1997).

Wolf spiders (Family Lycosidae) have been used as models to study the evolution and function of communication, particularly the genus *Schizocosa* (Ahtiainen et al., 2003; Ahtiainen et al., 2004; Ahtiainen et al., 2005; Hebets, 2005; Hebets and Uetz, 1999; Hebets and Uetz, 2000; Kotiaho et al., 1998; Miller et al., 1998; Parri et al., 2002; Rivero et al., 2000; Scheffer et al., 1996; Stratton and Uetz, 1983; Stratton and Uetz, 1986; Taylor et al., 2005; Uetz and Roberts, 2002; Uetz and Stratton, 1982). Wolf spider males communicate to females using multimodal displays often consisting of chemical, visual and seismic (vibratory) components (Hebets, 2005; Hebets and Uetz, 1999; Hebets and Uetz, 2000; Roberts and Uetz, 2004; Roberts and Uetz, 2005; Scheffer et al., 1996; Taylor et al., 2005; Uetz and Roberts, 2002). In particular, seismic components have special relevance as the majority of spiders use vibrations as the predominant modality guiding behavior (Barth, 1985; Barth, 1998; Barth, 2002; Foelix, 1996; Uetz and Stratton, 1982). Seismic signals produced by males during courtship displays have been shown to be important in mate choice and species recognition (Hebets, 2005; Hebets and Uetz, 1999; Parri et al., 2002; Rivero et al., 2000; Uetz and Stratton, 1982). Despite this importance, seismic signals in *Schizocosa* remain poorly understood and very few studies have examined the mechanisms used to produce seismic signals (Rovner, 1967; Rovner, 1975).

Using the novel technique of high-speed cinematography, Rovner showed that, contrary to the widely held belief that wolf spiders produced sounds by percussion, some wolf spiders produced seismic signals by stridulation (Rovner, 1975). Subsequent studies found evidence for stridulatory apparatuses in other wolf spiders (Fernandez-Montraveta and Simo, 2002). Recent developments in non-contact vibration recording techniques as well as synchronized high-speed videography provide powerful tools to re-examine seismic signal production mechanisms in wolf spiders (Elias et al., 2003; Nieh and Tautz, 2000). In this study, we examined the signal-production mechanisms of the wolf spider *Schizocosa stridulans* Stratton.

Materials and methods

Spiders

Immature male and female *Schizocosa stridulans* were collected at night from two sites in Marshall County in northern Mississippi, USA, on 6 and 7 May 2005. All spiders were brought back to the laboratory, where they were housed individually, provided with a constant source of moisture and fed 3–5 crickets once a week.

Recording procedures

Courtship arenas were constructed by stretching nylon fabric on a circular 26.5 cm needlepoint frame. We used an artificial courting substrate in order to facilitate synchronous high-speed video and laser vibrometer recordings. In the field, males are found in deciduous forests on a substratum composed of complex leaf litter, but no differences have been observed in male courtship behavior on natural *versus* artificial substrates (E.A.H., personal observation). We characterized the nylon fabric and determined that the nylon substrate passed all frequencies in the animal's signaling bandwidth equally (data not shown). A virgin female was confined overnight on the arena to deposit silk. Silk has been shown to be an effective releaser of male courtship in many *Schizocosa* species in both natural and artificial substrates (Stratton, 1983; Stratton, 1997; Stratton and Uetz, 1983; Stratton and Uetz, 1986). A total of eight different virgin females was used. At the beginning of every recording session, females were removed and, subsequently, males placed in the arena. Recording started when males began courting. We recorded substrate vibrations produced during courtship using a laser doppler vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head; Walbronn, Germany) (Michelsen et al., 1982). A piece of reflective tape (approx. 1 mm^2) was attached at the centre of the arena to serve as a measurement point for the LDV. The LDV signal was synchronized with two concurrent methods of video recording. (1) The LDV signal was recorded on the audio track during standard videotaping of courtship behavior (Navitar Zoom 7000 lens; Rochester, NY, USA; Panasonic GP-KR222; Matsushita Electric Industrial Co., Osaka, Japan; Sony DVCAM DSR-20 digital VCR; Tokyo, Japan; 44.1 kHz audio sampling rate). (2) The LDV signal was digitized (National Instruments PCI-6023E; Austin, TX, USA; 10 kHz sampling rate) simultaneously with the capture of digital high-speed video (500 frames s^{-1}; RedLake Motionscope PCI 1000; San Diego, CA, USA) using Midas software (v.2.0; Xcitex, Inc., Cambridge, MA, USA). All recordings were made on a vibration-isolated table. At the conclusion of each recording session, females were confined to arenas to deposit fresh silk.

Experimental manipulations

Recordings of seismic signals were made from each male prior to experimental manipulation. We manipulated males by either (1) preventing palpal movement by waxing the tibio–cymbial joint using a mixture of beeswax and colliphonium, (2) preventing abdominal (opisthosoma) movements by attaching the cephalothorax (prosoma) to the abdomen with wax or (3) manipulating both the cephalothorax–abdominal joint and the palpal tibio-cymbial joint. To ensure that these treatments did not affect normal locomotory activities, we waited two days following these manipulations and observed whether or not animals were able to successfully capture prey. We used only males that were able to capture prey during this interval.

Sound and video analysis

Complete courtships of 30 different males were recorded. Seismic courtship signal displays can be divided into two distinct categories: (1) 'rev' displays ('pulses' in Stratton, 1997) and (2) 'idle' displays ('trills' in Stratton, 1997). Examples were selected for detailed analysis. Body movements for an individual were measured from digital high-speed video using Midas software. Power spectra of vibratory signals were calculated using Matlab software (v.7.1; The Mathworks, Natick, MA, USA) and 2–3 signals averaged for each individual. Spectrograms were made using Raven (Cornell University, Lab of Ornithology). Males frequently changed position when producing seismic signals (see below), hence it was difficult to maintain the laser at a constant distance from the courting male. Although there were differences in the attenuation of signals depending on a male's final courting position, attenuation characteristics were similar for all frequencies, hence peak frequency measurements were not significantly distorted and, furthermore, comparisons of different signal conditions were based on normalized spectra (see below).

Power spectra analysis

Within a treatment set (control, experimental) from an individual animal, individual signals (see below) were identified using videotaped data, and a random selection of each seismic signal display acquired. Normalized power spectra of rev displays were then calculated using the pwelch function in Matlab. Peak intensities were measured for low- (0–500 Hz) and high-frequency (500–3000 Hz) bands. Within treatment sets for each individual, intensity was normalized to the highest intensity produced. Differences between treatment sets were tested for significance ($P<0.05$) using a paired *t*-test. Statistical tests were conducted using the Systat statistical analysis package (SSI, Richmond, CA, USA).

Scanning electron microscopy

Palps were dissected to separate the joint between the tarsus and cymbium. Specimens were dehydrated by a series of increasing ethanol concentrations (10, 30, 50, 60, 70, 80, 90 and 95%) for 20 min in each solution. Following dehydration, they were mounted on a 12.7 mm-diameter aluminum stub (Canemco-Marivac part # 700-1; Quebec, Canada) with doubled-sided adhesive tape (3M$^{\text{TM}}$ Scotch No. 655) and gold sputter coated with a Polaron SEM coating unit PS3 (Watford, UK). Specimens were viewed at 20 keV using Hitachi SEM model S-530 (Tokyo, Japan) and photographed onto 35 mm Fujifilm Neopan 100 black-and-white film with a Nikon FG-20 camera.

Results

Rev courtship displays

Signal characteristics

Courtship behavior began when males encountered silk, presumably containing female pheromones. Males would often chemo-explore by rubbing the dorsum of their palps against the substrate. Following chemo-exploration, males assumed a courtship posture where all the legs were spread widely apart and the palps were placed perpendicular to the arena surface (a in Fig. 1Bi). After this position was assumed, male spiders flexed the distal joint of the palp repeatedly (b–c in Fig. 1Bi). This subtle flexion corresponded with a burst of high-frequency, broadband seismic vibrations (peak frequency 1045±47.33 Hz, mean ± s.e.m.; range 450–2402 Hz; N=67 signals from 25 males). Palp flexions occurred at a frequency of 80±3.0 Hz, mean ± s.e.m. (N=5 individuals). Coincident with palp flexion and the production of these high-frequency components, dorso-ventral tremulations of the abdomen occurred that corresponded with low-frequency seismic components. Abdominal vibrations occur at a frequency of 33±6 Hz (mean ± s.d., N=10 males) and consist of 2–3 abdominal flexions (c–d in Fig. 1Bi). Each individual abdominal flexion is also associated with subtle decaying oscillation ('ringing') at a frequency of about 75±4 Hz (mean ± s.d., N=10 males). Abdominal movements correspond with the production of low-frequency vibrations (peak frequency 105.79±6.97 Hz, mean ± s.e.m.; range 20–363 Hz; N=67 signals from 25 males). Palpal and abdominal seismic components are produced simultaneously for a brief period of time (abdominal tremulation begins before palpal flexion ceases, c in Fig. 1Bi) and both combine to produce the integrated signal. Integrated rev signals were 0.378±0.01 s (mean ± s.e.m.; range 0.209–0.490 s; N=67 from 25 males; Fig. 2A) in duration. Rev signals occur in bouts of 1–11 revs separated by 0.71±0.04 s (mean ± s.e.m.; N=30 for 15 males) of silence (Fig. 1A).

Experimental manipulations

Palpal movement. Analysis of high-speed videos suggests that high-frequency components are produced by flexions of the tibio-cymbial joint of the palp and not by abdominal movements, and this is consistent with previous descriptions of a stridulatory signal in this genus (Rovner, 1975). Males were recorded prior to treatment, and then with the tibio-cymbial joint of the palp immobilized (Fig. 2B). We could readily identify the occurrence of each signal type by the postures and movement characteristics of each signal from videotapes (Fig. 1Bi).

When palpal flexion was prevented, higher frequency components of rev signals were attenuated while lower frequencies were not (Figs 2B, 3A). No significant differences were observed for low-frequency peaks between control and experimental treatments (low-frequency control treatment –7.089±2.692 dB, mean ± s.d.; low-frequency experimental treatment –4.975±1.604 dB, mean ± s.d.; N=5, $t_{1,4}$=–1.734, P=0.158; Fig. 3A). Significant differences were observed for high-frequency peaks between control and experimental treatments (high-frequency control treatment –11.273± 5.179 dB, mean ± s.d.; high-frequency experimental treatment –38.507±3.812 dB, mean ± s.d.; N=5, $t_{1,4}$=8.816, $P<0.001$; Fig. 3A). Low-frequency components of the signal remained, consisting of vibrations of 0.240±0.011 s (mean ± s.e.m., N=20 from 5 males) in duration and of low frequency (80.18±11.45 Hz, mean ± s.e.m.; range 23–244 Hz; N=17 from 5 males).

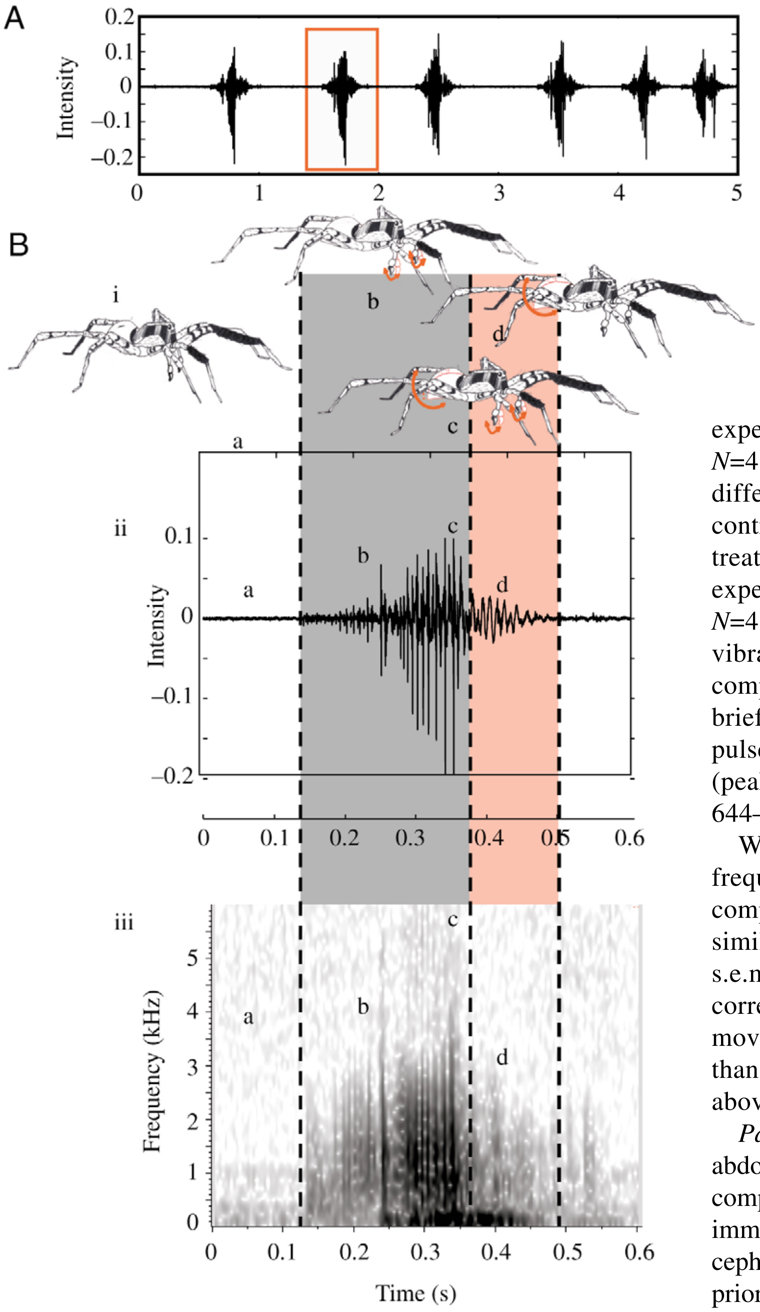

Fig. 1. Seismic rev displays of *Schizocosa stridulans*. (A) Bout of rev displays. (B) Detail from red box in A. Top panel (i) shows body positions, with letters (a–d) illustrating movements of the palpal tibio-cymbial joint and abdomen. Middle panels (ii) show the oscillogram of rev displays. Bottom panels (iii) show a spectrogram of rev displays. Panels are shown in the same time scale, with letters (a–d) corresponding to the body movements illustrated in i. Signals begin with a flexion of the palpal tibio-cymbial joint (b–c) followed by abdominal vibrations (c–d). Palpal movements correspond to the production of high frequencies, and abdominal movements correspond with the production of low frequencies.

Abdominal movement. Analysis of high-speed videos suggested that low-frequency components are produced by abdominal movements and not by flexions of the tibio-cymbial joint of the palp. Males were recorded both prior to and after abdomen immobilization (Fig. 2C). We were readily able to identify the attempted production of each seismic signal component by the postures and movement of males from the videotape (Fig. 1Bi).

When abdominal movements were prevented, lower frequency components of rev signals were attenuated while higher frequencies were not (Figs 2C,3B). Significant differences were observed for low-frequency peaks between control and experimental treatments (low-frequency control treatment –4.553±1.303 dB, mean ± s.d.; low-frequency experimental treatment –14.927±6.223 dB, mean ± s.d.; N=4, $t_{1,3}$=4.117, P=0.026; Fig. 3B). No significant differences were observed for high-frequency peaks between control and experimental treatments (high-frequency control treatment –14.651±8.069 dB, mean ± s.d.; high-frequency experimental treatment –18.650±6.177 dB, mean ± s.d.; N=4, $t_{1,3}$=1.163, P=0.329; Fig. 3B). Examining the vibrations produced after manipulation showed that components produced during palpal flexion are a train of brief 0.262±0.012 s (mean ± s.e.m., N=17 from 5 males) pulses of relatively broadband, high-frequency vibrations (peak frequency 890±65.48 Hz, mean ± s.e.m.; range 644–2186 Hz; N=20 from 5 males).

While preventing abdominal movements attenuated low-frequency signal components, they were not eliminated completely. A low-frequency peak was still observed at a similar frequency to intact signals (80.17±11.45, mean ± s.e.m., N=17 from 5 males). This weaker low-frequency peak corresponded to vibrations produced by the gross movements of the palps – the rate of palpal flexions rather than the stridulation generated by these movements (see above).

Palpal and abdominal movement. In order to test whether abdominal and palpal movements were sufficient to explain all components of rev seismic signals in *S. stridulans*, we immobilized both the tibio-cymbial joint of the palp and the cephalothorax–abdomen joint (Fig. 2D). Males were recorded prior to treatment, then with palps and abdomen immobilized. We could readily identify the occurrence of each signal type by the postures and movement characteristic of each signal from videotapes (Fig. 1Bi).

All components of rev signals were attenuated following experimental manipulation (Figs 2D, 3C). Significant differences were observed for low-frequency peaks (low-frequency control treatment –4.444±1.590 dB, mean ± s.d.; low-frequency experimental treatment –24.536±5.339 dB, mean ± s.d.; N=5, $t_{1,4}$=–8.574, P=0.001; Fig. 3C) and high-frequency peaks (high-frequency control treatment –8.218±1.488 dB, mean ± s.d.; high-frequency experimental treatment –39.093±7.960 dB, mean ± s.d.; N=5, $t_{1,4}$=8.703, P=0.001; Fig. 3C) between control and experimental treatment. Hence, palpal and abdominal movements are sufficient to produce multi-component rev signals.

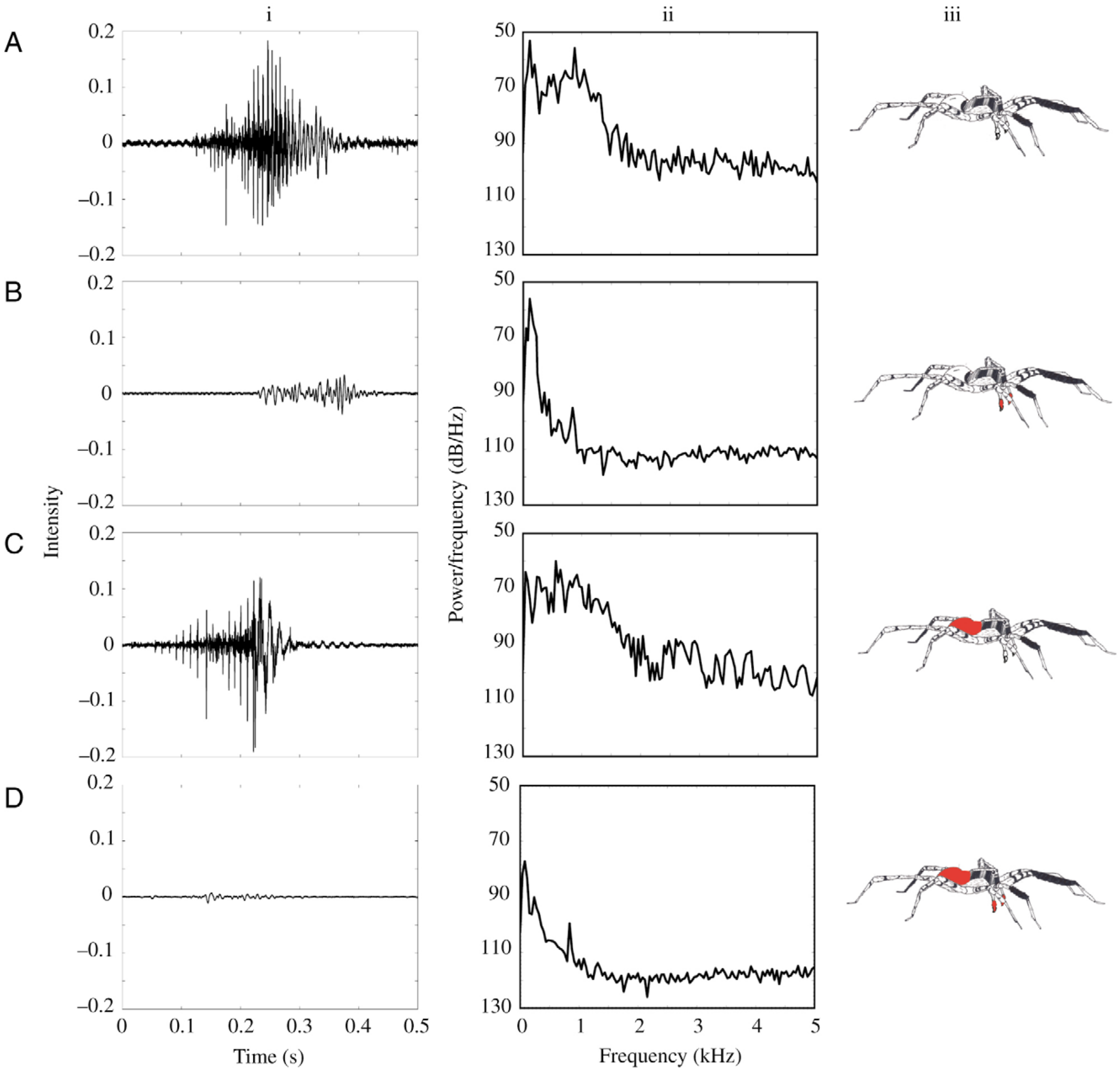

Fig. 2. Effects of male experimental manipulation on power spectra of rev displays. (i) Oscillogram of rev display; (ii) power spectra of rev display; (iii) experimental treatment. (A) Control treatment. (B) Palpal treatment. Experimental treatment consisted of waxing the tibio-cymbial joint of the palp, rendering the joint immovable. High frequencies were attenuated following manipulation. (C) Abdominal treatment. Experimental treatment consisted of waxing the cephalothorax–abdomen joint, rendering the joint immovable. Low frequencies were attenuated following manipulation. (D) Palpal and abdominal treatment. Experimental treatment consisted of waxing the tibio-cymbial joint of the palp and waxing the cephalothorax–abdomen joint, rendering both joints immovable relative to each other. All signals were attenuated following manipulation.

Idle courtship displays

Signal characteristics

The predominant seismic displays observed in this study were rev displays. Males, however, also produced another type of signal, idle displays (‘trill’ in Stratton, 1997). Males assumed a courtship posture where all the legs were spread widely apart and the palps were placed perpendicular to the arena surface. The male then positioned its forelegs in an arched position above the arena and quickly tapped its legs on the substrate (percussion; Fig. 4i). Four to 11 individual leg taps occurred in rapid succession. Leg taps are audible to the human ear (Stratton, 1997). After the leg taps, male spiders rapidly flexed the distal joint of the palp (Fig. 4ii). Individual palps were flexed out of phase to produce a sustained series of brief seismic pulses (duration 3.32±0.757 s, mean ± s.e.m.; range 0.5–9.4 s; *N*=16 from 8 males). This movement corresponded with high-frequency, broadband seismic vibrations (peak frequency 950±127.29 Hz, mean ± s.e.m.; range 450–1250 Hz; *N*=16 from

8 males) similar to rev displays. No abdominal vibrations were observed during idle displays. Low-frequency components appeared to have been caused by the rate of palpal flexion.

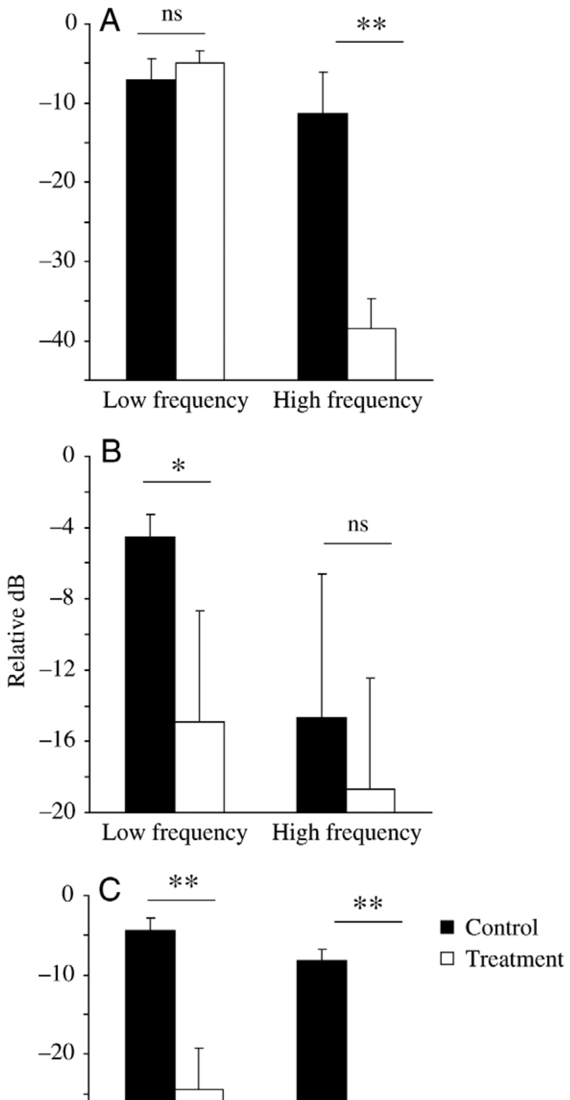

Fig. 3. Effects of experimental treatments on rev displays. Within treatment pairs (control and experimental), peak intensities were normalized to the maximum intensity produced. Graphs show average dB differences for each treatment type. (A) Palpal treatment. Experimental treatment attenuated high frequencies (**$P<0.001$, paired *t*-test). No significant difference was observed for low frequencies (ns, not significant). (B) Abdominal treatment. Experimental treatment attenuated low frequencies (*$P<0.05$, paired *t*-test). No significant difference was observed for high frequencies (ns). (C) Palpal and abdominal treatment. Experimental treatment attenuated both low and high frequencies (**$P<0.001$, paired *t*-test).

Experimental manipulations

Idle displays did not occur in all the individuals recorded, hence it was not possible to perform statistical analyses on control and experimental treatments. We recorded idle displays whenever possible and present individual examples of idle displays from all treatment groups. When the palpal tibio-cymbial joint was immobilized, signals were greatly attenuated (Fig. 5B). When abdomens were immobilized, no differences were observed, although low-frequency components were slightly attenuated (Fig. 5C). When both palps and abdomens were immobilized, signals were greatly attenuated (Fig. 5D). Idle displays are thus produced predominantly by the palps, and flexion of the palpal tibio-cymbial joint is sufficient to explain idle displays.

SEM of stridulatory organs

The observation that high-frequency signal components require flexion of body parts that move relative to each other suggests a stridulatory mechanism (Dumortier, 1963; Rovner, 1975; Stratton, 1997). Therefore, we examined, using scanning electron microscopy (SEM), the palpal tibio-cymbial joint (Fig. 6A) of males (Rovner, 1975). SEMs revealed a presence of a hardened scraper on the dorsal surface of male cymbium (Fig. 6B). In the apposing tibial area, we noted the presence of a file on the dorsal base of the tarsus (Fig. 6C).

Discussion

The courtship displays of *S. stridulans*, similar to those of jumping spiders of the genus *Habronattus* (Elias et al., 2003; Elias et al., 2004; Elias et al., 2005), comprise multiple seismic components that are produced by independent mechanisms. In addition, in some cases multiple components are produced simultaneously (parallel multi-component displays) while in other cases multiple components are produced in a temporal series (serial multi-component displays). Alternative modes of combining multiple signal components may be an important factor in signal function, but also one that is constrained by the mechanisms and structures involved in the production. The type and location of sound-producing structures as well as the sound-production mechanism used can give insight into the mechanisms driving signal evolution. Several basic arrangements are possible for structures involved in the production of multi-component signals. Individual components may be produced by (1) the same structure, (2) bilaterally similar but independent structures or (3) completely independent structures. In addition, signals using these structures can be produced using (1) the same mechanism or (2) multiple mechanisms. A typical example of signals using a single structure and mechanism is the katydid *Metrioptera sphagnorum*, where multiple signal components are all produced by a forewing file-and-scraper mechanism (stridulation) but different signal components are produced by different parts of the file (Morris and Pipher, 1972). An example of multi-component signals produced using similar structures but independent mechanisms is jumping spiders that

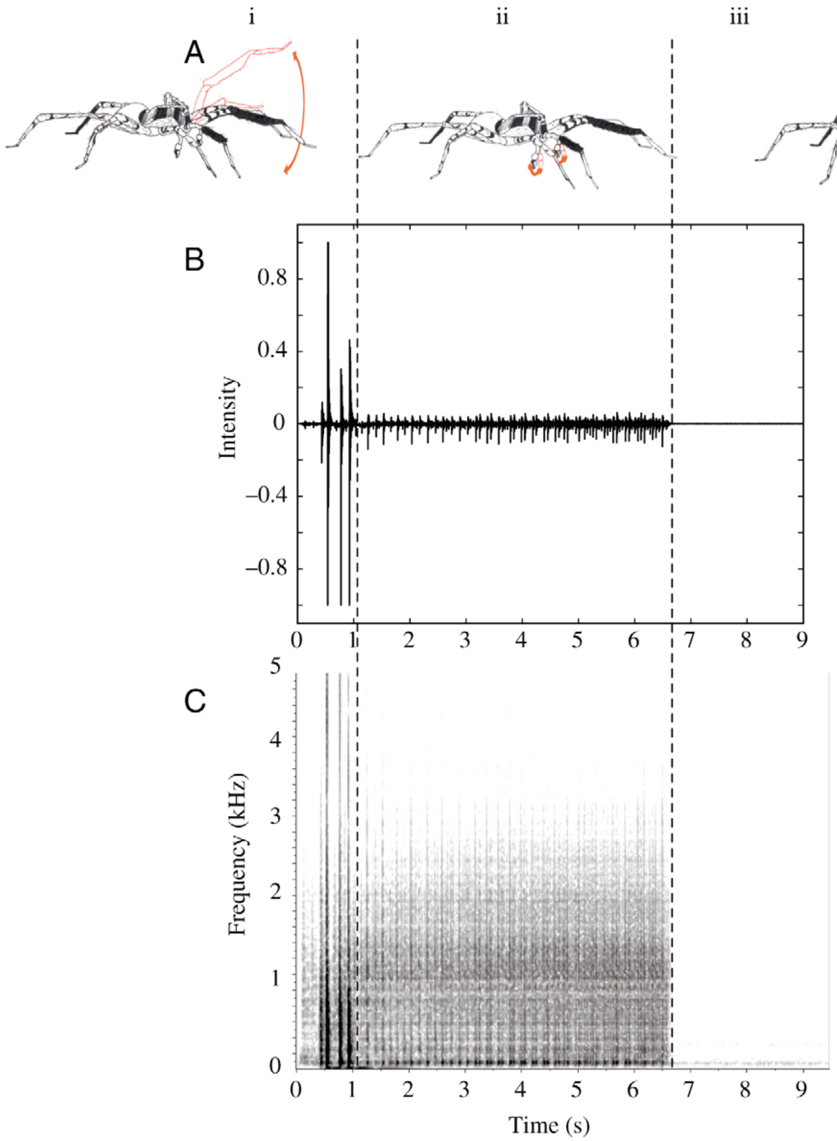

Fig. 4. Seismic idle displays of *Schizocosa stridulans*. (A) Body positions with columns (i–iii) illustrating movements of the palpal tibio-cymbial joint. (B) Oscillogram of idle displays. (C) Spectrogram of idle displays. Panels are shown in the same time scale, with columns corresponding to the body movements illustrated in A. Signals begin with leg tapping, followed by flexions of the palpal tibio-cymbial joint. Palpal movements correspond to the production of high frequencies.

produce seismic signal components using abdominal movements alone (tremulation) and abdominal movements coupled to a frequency multiplier (stridulation) (Elias et al., 2003). Examples of independent bilaterally symmetrical structures used to produce multi-component signals include song birds that produce signals using a pair of syringeal vibrators, each of which can potentially produce harmonically unrelated sounds at once (Bradbury and Vehrencamp, 1998; Goller and Suthers, 1995; Suthers, 1990; Suthers et al., 2004; Suthers and Zollinger, 2004), and grasshoppers that stridulate using structures found on both hind legs (Elsner and Wasser, 1995; von Helversen et al., 2004). Wolf spiders (present study) also stridulate using bilaterally symmetrical palps. Independent bilaterally symmetrical structures usually produce sounds using the same mechanism.

In this study, wolf spiders use independent structures including palps, abdomen and forelegs to produce multi-component songs. In addition, each structure produces components using a different mechanism (stridulation, tremulation and percussion). Such signals are presumably costly to produce since animals must develop and coordinate completely different structures and neuromuscular systems. Male *S. stridulans* court females on natural substrates of leaf litter (E.A.H., unpublished observation), and courtship signals must often propagate through multiple leaves, where signals may become distorted and attenuated due to filtering, reflection and scattering. There is often no simple relationship between the amplitude of the signal and the distance from the sender along single leaf surfaces (Barth, 2002; Cokl et al., 2004; Magal et al., 2000; Michelsen et al., 1982) and this presumably becomes more complex as signals propagate through multiple leaves. Given this signaling environment, knowledge of seismic signal-production mechanisms can provide insights regarding multi-component signal function.

A high-bandwidth signal may be a way to ensure that some part of a signal is detected by the receiver in a complex signaling environment with unpredictable filtering properties (redundant backups) (Iwasa and Pomiankowski, 1994;

Johnstone, 1996; Pomiankowski and Iwasa, 1993; Partan and Marler, 2005). Production of multiple components by the palps and abdomen may be a way to expand the bandwidth of seismic signals. This does not, however, explain why components are produced in parallel (see below). In addition, high bandwidths are a property of percussive signals, and percussion does not require coordination from multiple sources (i.e. less costly to produce). If selection has acted to increase signal bandwidth, then one would predict that percussive components should dominate signals. In this species of wolf spiders, percussion only occurs in idle and not rev displays. This suggests that back-up signals alone are not sufficient to explain *S. stridulans* seismic signals.

The location of distinct, independent sound-production areas in *S. stridulans* suggests that males may be transmitting non-redundant/multiple messages (Iwasa and Pomiankowski, 1994; Johnstone, 1996; Pomiankowski and Iwasa, 1993; Partan and Marler, 2005). Multiple messages hypotheses propose that multiple signal components relay different information to receivers. For example, the stridulatory apparatus located on the palpal tibio-cymbial joint is developmentally fixed at maturation and may provide more static information about

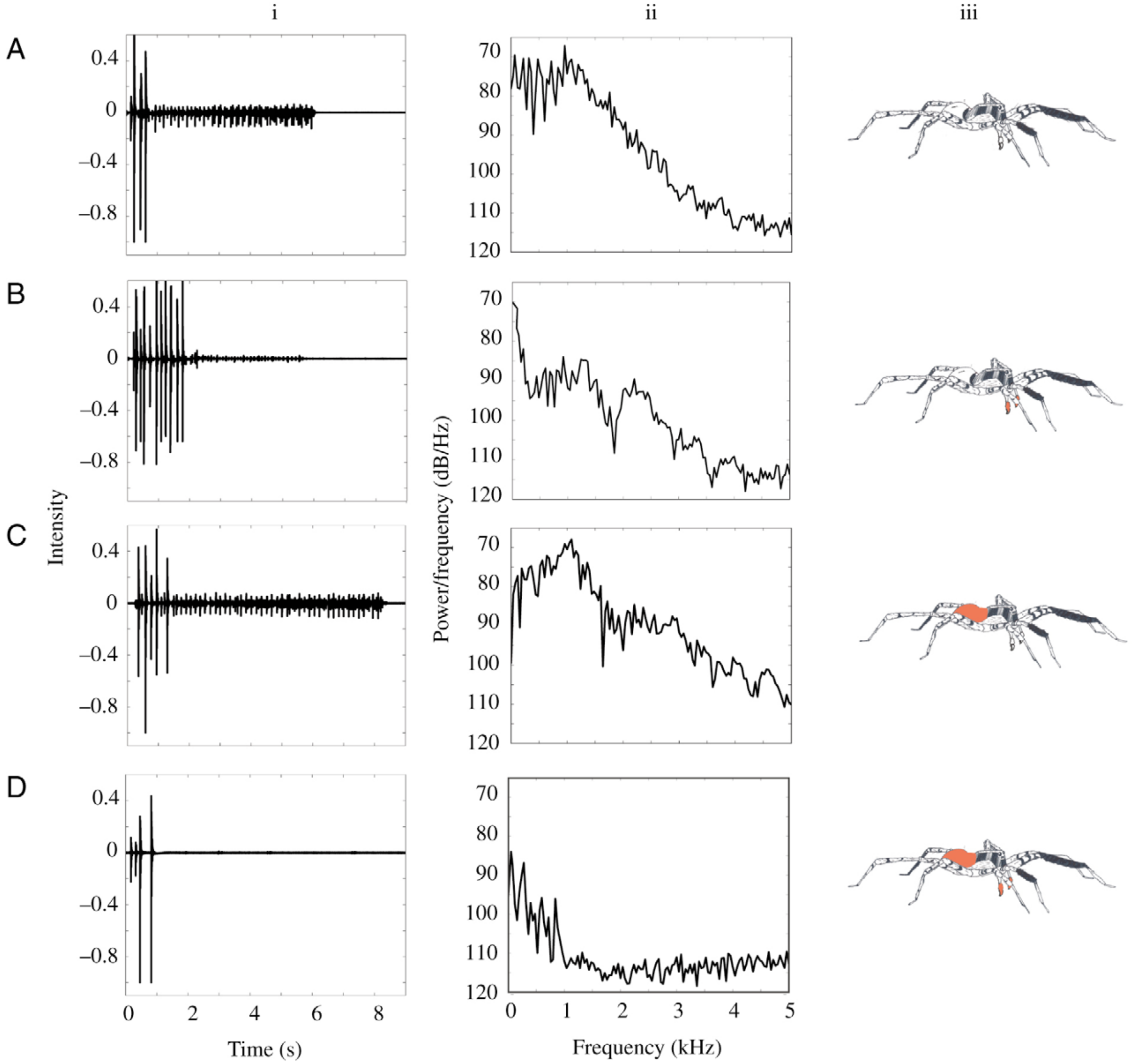

Fig. 5. Effects of male experimental manipulation on power spectra of idle displays. (i) Oscillogram of idle display; (ii) power spectra of idle display; (iii) experimental treatment. (A) Control treatment. (B) Palpal treatment. Experimental treatment consisted of waxing the tibio-cymbial joint of the palp, rendering the joint immovable. Percussive components were unaffected while stridulatory components were attenuated following manipulation. (C) Abdominal treatment. Experimental treatment consisted of waxing the cephalothorax–abdomen joint, rendering the joint immovable. No seismic components were affected following manipulation. (D) Palpal and abdominal treatment. Experimental treatment consisted of waxing the tibio-cymbial joint of the palp and waxing the cephalothorax–abdomen joint, rendering both joints immovable relative to each other. Percussive components were unaffected while stridulatory/tremulation components were attenuated following manipulation.

male quality such as overall size. By contrast, abdomen size is not fixed but is dependent on the recent feeding history of the male, potentially providing more dynamic information about male quality such as foraging success. Since the rev displays of *S. stridulans* consist of both a high- and a low-frequency component, males may be able to code for information about both long-term (developmental) quality (high-frequency component) and short-term quality (low-frequency component). Females attending to the rev display would then be gaining information about multiple aspects of a male's condition. Idle displays, on the other hand, are produced using leg percussion and palpal stridulation but not abdominal tremulations. Idle displays are much longer in duration but occur rarely. It is possible that idle displays provide further information about long-term (developmental) quality. Leg taps (and presumably idle displays) occur more frequently immediately prior to mounting and copulation of a female (Stratton, 1998), hence idle displays may function as short-distance signals since males producing long-duration signals may risk interference from other male signals (see below). Leg taps may function as an attention primer to the long-duration stridulatory component, as has been suggested in other spiders (Elias et al., 2003). Further experiments are necessary to test these hypotheses, with special consideration of signal quality at different distances from courting males, as courting substrates can heavily influence signal characteristics (Cokl et al., 2004; Cokl et al., 2005; Elias et al., 2004; Magal et al., 2000; Michelsen et al., 1982).

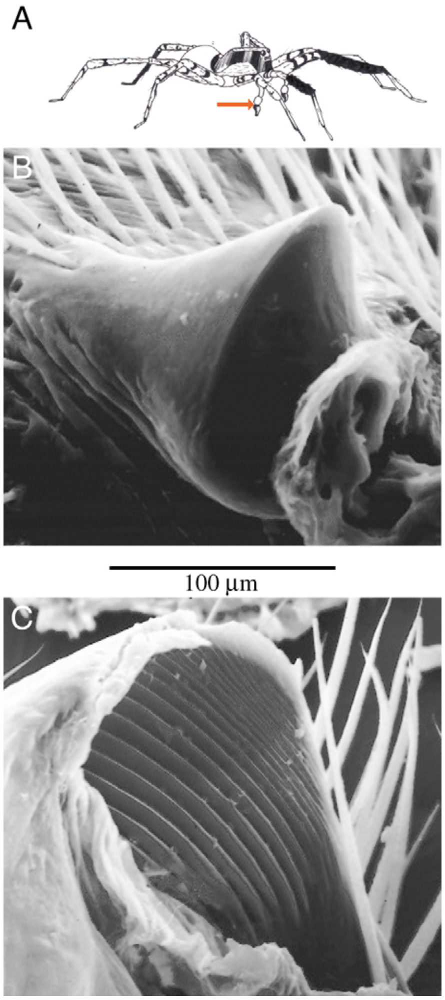

Fig. 6. SEM of tibio-cymbial joint on the male palp of *S. stridulans*. (A) *S. stridulans* courtship posture. Arrow shows position of the tibio-cymbial joint. (B) Scraper on the dorsal surface of male cymbium. (C) File on the inner ventral surface of the base of the tarsus.

Alternatively, multi-component signal evolution may be driven by inter-component interactions (Hebets and Papaj, 2005). Many types of seismic signals (i.e. bending waves) have the property of dispersive propagation – different frequencies travel at different speeds (Aicher and Tautz, 1990; Barth, 2002; Cremer et al., 1973; Michelsen et al., 1982). It is therefore theoretically possible that if wolf spiders use bending waves to communicate, wolf spider females can locate potential mates by measuring arrival-time differences of low- and high-frequency signal components, as has been shown in scorpions (Brownell and Farley, 1979; Brownell, 1977; Brownell and Van Hemmen, 2000). Further studies are necessary to demonstrate such a function in *S. stridulans*.

While the above hypotheses focus mainly on signal-producing structures, we can also generate hypotheses about signal function based on the timing of multiple components (i.e. serial or parallel). Serial displays are very common in the animal communication literature. For example, multiple syllable types in birds (Catchpole and Slater, 1995), insect songs (Guerra and Morris, 2002) and jumping spiders (Elias et al., 2003). Serial multi-component signals may evolve in systems that favor sequential assessment of signals, for example birds, where repertoire size is a measure of male quality (Catchpole and Slater, 1995), or when one signal component acts as an amplifier to another (Hasson, 1991).

Parallel multi-component signals are less common in the literature and refer to components that are produced concurrently resulting in an integrated signal (in terms of timing). In this study, wolf spiders produce rev displays using a combination of abdominal tremulations and palpal stridulation slightly offset in time but produced concurrently. Some bugs, crabs and katydids also appear to produce parallel signals (Cokl and Doberlet, 2003; Cokl et al., 2004; Gogala, 1985; Kalmring, 1985; Kalmring, 1997; Moraes et al., 2005; Popper et al., 2001; Virant-Doberlet and Cokl, 2004). Identification of parallel multi-component signals requires a detailed analysis of sound-production mechanisms and it is possible that parallel multi-component signals are common.

The selective forces that may drive the evolution of serial *versus* parallel multi-component signals have not been addressed in the literature. Parallel signals may evolve under selection for increased information content in systems where communication occurs under time constraints. The threats of eavesdropping by predators or interference by competitors may limit available signaling time for male *S. stridulans*. Additionally, pre-copulatory sexual cannibalism is relatively common in *S. stridulans* (E.A.H., unpublished data) and males must rapidly identify themselves as potential mates to avoid a predatory response from females. Pre-copulatory sexual cannibalism may thus impose strong selection favoring rapid information transfer in male courtship thorough parallel multi-component signaling.

S. stridulans males also intermittently produce serial signals (idle displays). The rarity of idle displays may reflect selection against long-duration signals. In addition, idle displays occur more frequently when males and females are in close proximity (Stratton, 1998). In these circumstances, interference from rival male signals may be reduced. Theoretical models of multiple signal evolution have shown that, with increasing costs, signals should evolve to be simpler and unicomponent (Iwasa and Pomiankowski, 1994; Pomiankowski and Iwasa, 1993; Pomiankowski and Iwasa, 1998). The present study suggests an alternative where increasing costs of assessment and/or signaling do not lead to simplification but instead to the economization of signals by parallel multi-component signal production.

Alternatively, a parallel multi-component signal could arise through a co-evolutionary elaboration of a simple (unicomponent) signal. In *S. stridulans*, abdominal tremulations occur at the same frequency as palpal flexions and appear to amplify low-frequency components produced incidentally by stridulatory movements. It is possible that in an ancestral unicomponent stridulating species, low frequencies produced by body flexions were an informative cue to females since larger animals can induce larger vibrations. Males could then evolve abdominal tremulation as an exaggeration of the incidental body movement cue. Parallel multi-component signals could thus reflect an ancestral origin and could persist in wolf spiders since abdominal tremulations appear to function to increase the intensity of low-frequency components.

In summary, detailed knowledge of sound-production mechanisms is necessary in discussions of signal design and evolution. First, the location and types of sound-production mechanisms can offer insights into hypotheses on signal evolution and function. Second, the majority of work on multiple signals has focused on signals that are easily discriminated by humans, i.e. either multimodal signals or serial multi-component signals. As a result, little work has been conducted on parallel multi-component signals as they require detailed knowledge of sound-producing mechanisms. Parallel multi-component signals are a major category of multiple signals and more detailed knowledge is required to determine the frequency of such signals in nature as well as to illuminate the selective pressures that drive the evolution of different types of multiple signals (multimodal *vs* parallel multi-component *vs* serial multi-component).

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References

Ahtiainen, J. J., Alatalo, R. V., Mappes, J. and Vertainen, L. (2003). Fluctuating asymmetry and sexual performance in the drumming wolf spider *Hygrolycosa rubrofasciata*. *Ann. Zool. Fennici* **40**, 281-292.

Ahtiainen, J. J., Alatalo, R. V., Mappes, J. and Vertainen, L. (2004). Decreased sexual signalling reveals reduced viability in small populations of the drumming wolf spider *Hygrolycosa rubrofasciata*. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 1839-1845.

Ahtiainen, J. J., Alatalo, R. V., Kortet, R. and Rantala, M. J. (2005). A trade-off between sexual signalling and immune function in a natural population of the drumming wolf spider *Hygrolycosa rubrofasciata*. *J. Evol. Biol.* **18**, 985-991.

Aicher, B. and Tautz, J. (1990). Vibrational communication in the Fiddler Crab, *Uca pugilator*. 1. Signal transmission through the substratum. *J. Comp. Physiol. A* **166**, 345-353.

Bailey, W. J. and Rentz, D. C. F. (1990). *The Tettigoniidae: Biology, Systematics and Evolution.* Bathurst (Australia): Crawford House.

Barth, F. G. (1985). Neuroethology of the spider vibration sense. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 203-229. New York: Springer-Verlag.

Barth, F. G. (1998). The vibrational sense of spiders. In *Comparative Hearing: Insects* (ed. R. R. Hoy, A. N. Popper and R. R. Fay), pp. 228-278. New York: Springer.

Barth, F., G. (2002). *A Spider's World: Senses and Behavior.* Berlin: Springer-Verlag.

Bostwick, K. S. and Prum, R. O. (2005). Courting bird sings with stridulating wing feathers. *Science* **309**, 736.

Bradbury, J. W. and Vehrencamp, S. L. (1998). *Principles of Animal Communication.* Sunderland (MA): Sinauer Association.

Brownell, P. H. (1977). Compressional and surface-waves in sand used by desert scorpions to locate prey. *Science* **197**, 479-482.

Brownell, P. and Farley, R. D. (1979). Orientation to vibrations in sand by the nocturnal scorpion *Paruroctonus mesaensis* – mechanism of target localization. *J. Comp. Physiol.* **131**, 31-38.

Brownell, P. H. and Van Hemmen, J. L. (2000). Vibration sensitivity and prey-localizing behaviour of sand scorpions. *Am. Zool.* **40**, 955-956.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biol. Rev.* **78**, 575-595.

Catchpole, C. K. and Slater, P. J. B. (1995). *Bird Song. Biological Themes and Variations.* Cambridge: Cambridge University Press.

Cokl, A. and Doberlet, M. V. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annu. Rev. Entomol.* **48**, 29-50.

Cokl, A., Presern, J., Virant-Doberlet, M., Bagwell, G. J. and Millar, J. G. (2004). Vibratory signals of the harlequin bug and their transmission through plants. *Physiol. Entomol.* **29**, 372-380.

Cokl, A., Zorovic, M., Zunic, A. and Virant-Doberlet, M. (2005). Tuning of host plants with vibratory songs of *Nezara viridula* L. (Heteroptera: Pentatomidae). *J. Exp. Biol.* **208**, 1481-1488.

Cremer, L., Heckl, M. and Ungar, E. E. (1973). *Structure-Borne Sound.* Berlin: Springer-Verlag.

Dumortier, B. (1963). Sound emissions in Arthropoda. In *Acoustic Behavior of Animals* (ed. R. G. Busnel), pp. 277-338. Amsterdam, London, New York: Elsevier.

Elias, D. O., Mason, A. C., Maddison, W. P. and Hoy, R. R. (2003). Seismic signals in a courting male jumping spider (Araneae: Salticidae). *J. Exp. Biol.* **206**, 4029-4039.

Elias, D. O., Mason, A. C. and Hoy, R. R. (2004). The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae). *J. Exp. Biol.* **207**, 4105-4110.

Elias, D. O., Hebets, E. A., Hoy, R. R. and Mason, A. C. (2005). Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae:Salticidae). *Anim. Behav.* **69**, 931-938.

Elsner, N. and Wasser, G. (1995). Leg and wing stridulation in various populations of the gomphocerine grasshopper *Stenobothrus rubicundus* (Germar 1817). I. Sound patterns and singing movements. *Zoology* **98**, 179-190.

Ewing, A. W. (1989). *Arthropod Bioacoustics: Neurobiology and Behaviour.* Ithaca: Cornell University Press.

Fernandez-Montraveta, C. and Simo, M. (2002). Male pedipalpal stridulatory devices in neotropical wolf spiders and their possible role in systematics. *J. Arachnol.* **30**, 475-480.

Foelix, R. F. (1996). *The Biology of Spiders.* New York: Oxford University Press.

Gerhardt, H. C. and Huber, F. (2002). *Acoustic Communication in Insects and Anurans.* Chicago, London: The University of Chicago Press.

Gogala, M. (1985). Vibrational songs of land bugs and their production. In *Acoustic and Vibrational Communication in Insects* (ed. K. Kalmring and N. Elsner), pp. 143-150. Berlin, Hamburg: Paul Parey.

Goller, F. and Suthers, R. A. (1995). Implications for lateralization of bird song from unilateral gating of bilateral motor patterns. *Nature* **373**, 63-66.

Guerra, P. A. and Morris, G. K. (2002). Calling communication in meadow katydids (Orthoptera, Tettigoniidae): Female preferences for species-specific wingstroke rates. *Behaviour* **139**, 23-43.

Hasson, O. (1991). Sexual displays as amplifiers – practical examples with an emphasis on feather decorations. *Behav. Ecol.* **2**, 189-197.

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proc. Natl. Acad. Sci. USA* **100**, 13390-13395.

Hebets, E. A. (2005). Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behav. Ecol.* **16**, 75-82.

Hebets, E. A. and Uetz, G. W. (1999). Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (Aranerae: Lycosidae). *Anim. Behav.* **57**, 865-872.

Hebets, E. A. and Uetz, G. W. (2000). Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.* **47**, 280-286.

Hebets, E. A. and Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**, 197-214.

Huber, F., Moore, T. E. and Loher, W. (1989). *Cricket Behavior and Neurobiology.* Ithaca: Cornell University Press.

Iwasa, Y. and Pomiankowski, A. (1994). The evolution of mate preferences for multiple sexual ornaments. *Evolution* **48**, 853-867.

Johnstone, R. A. (1996). Multiple displays in animal communication: 'Backup signals' and 'multiple messages'. *Philos. Trans. Royal Soc. Lond. B Biol. Sci.* **351**, 329-338.

Kalmring, K. (1985). Vibrational communication in insects (reception and integration of vibratory information). In *Acoustic and Vibrational Communication in Insects* (ed. K. Kalmring and N. Elsner), pp. 127-134. Berlin: Paul Parey.

Kalmring, K. (1997). Acousto-vibratory communication in bushcrickets (Orthoptera: Tettigoniidae). *Entomologia Generalis* **21**, 265-291.

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S. and Rivero, A. (1998). Energetic costs of size and sexual signalling in a wolf spider. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 2203-2209.

Ladich, F. (2000). Acoustic communication and the evolution of hearing in fishes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**, 1285-1288.

Ladich, F. and Bass, A. H. (1998). Sonic/vocal motor pathways in catfishes: comparisons with other teleosts. *Brain Behav. Evol.* **51**, 315-330.

Legendre, R. (1963). L'audition et l'émission de sons chez les araneides. *Ann. Biol.* **2**, 371-390.

Magal, C., Scholler, M., Tautz, J. and Casas, J. (2000). The role of leaf structure in vibration propagation. *J. Acoust. Soc. Am.* **108**, 2412-2418.

Markl, H. (1983). Vibrational communication. In *Neuroethology and Behavioral Physiology* (ed. F. Huber and H. Markl), pp. 332-354. Berlin: Springer-Verlag.

Michelsen, A., Fink, F., Gogala, M. and Traue, D. (1982). Plants as transmission channels for insect vibrational songs. *Behav. Ecol. Sociobiol.* **11**, 269-281.

Miller, G. L., Stratton, G. E., Miller, P. L. and Hebets, E. A. (1998). Geographical variation in male courtship behaviour and sexual selection in wolf spiders of the genus *Schizocosa*. *Anim. Behav.* **56**, 937-951.

Moller, A. P. and Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167-176.

Moraes, M. C. B., Laumann, R. A., Cokl, A. and Borges, M. (2005). Vibratory signals of four Neotropical stink bug species. *Physiol. Entomol.* **30**, 175-188.

Morris, G. K. and Pipher, R. E. (1972). Relation of song structure to tegminal movement in *Metrioptera sphagnorum* (Orthoptera–Tettigoniidae). *Can. Entomol.* **104**, 977-985.

Nieh, J. C. and Tautz, J. (2000). Behaviour-locked signal analysis reveals weak 200–300 Hz comb vibrations during the honeybee waggle dance. *J. Exp. Biol.* **203**, 1573-1579.

Parri, S., Alatalo, R. V., Kotiaho, J. S., Mappes, J. and Rivero, A. (2002). Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate. *Behav. Ecol.* **13**, 615-621.

Partan, S. and Marler, P. (1999). Communication goes multimodal. *Science* **283**, 1272-1273.

Partan, S. R. and Marler, P. (2005). Issues in the classification of multimodal communication signals. *Am. Nat.* **166**, 231-245.

Patek, S. N. (2001). Spiny lobsters stick and slip to make sound. *Nature* **411**, 153-154.

Pomiankowski, A. and Iwasa, Y. (1993). Evolution of multiple sexual preferences by Fisher runaway process of sexual selection. *Proc. R. Soc. Lond. B Biol. Sci.* **253**, 173-181.

Pomiankowski, A. and Iwasa, Y. (1998). Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Natl. Acad. Sci. USA* **95**, 5106-5111.

Popper, A. N., Salmon, M. and Horch, K. W. (2001). Acoustic detection and communication by decapod crustaceans. *J. Comp. Physiol. A* **187**, 83-89.

Rivero, A., Alatalo, R. V., Kotiaho, J. S., Mappes, J. and Parri, S. (2000). Acoustic signalling in a wolf spider: can signal characteristics predict male quality? *Anim. Behav.* **48**, 188-194.

Roberts, J. A. and Uetz, G. W. (2004). Chemical signaling in a wolf spider: a test of ethospecies discrimination. *J. Chem. Ecol.* **30**, 1271-1284.

Roberts, J. A. and Uetz, G. W. (2005). Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Anim. Behav.* **70**, 217-223.

Rovner, J. S. (1967). Acoustic communication in a lycosid spider (*Lycosa Rabida* Walckenaer). *Anim. Behav.* **15**, 273-281.

Rovner, J. S. (1975). Sound production by Nearctic wolf spiders – Substratum-coupled stridulatory mechanism. *Science* **190**, 1309-1310.

Rovner, J. S. (1980). Vibration in *Heteropoda venatoria* (Sparassidae) – a 3rd method of sound production in spiders. *J. Arachnol.* **8**, 193-200.

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Anim. Behav.* **58**, 921-931.

Scheffer, S. J., Uetz, G. W. and Stratton, G. E. (1996). Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.* **38**, 17-23.

Stratton, G. E. (1983). Comparison of courtship behaviors and interspecific crosses in the *Schizocosa ocreata* species complex Araneae: Lycosidae. *Am. Zool.* **23**, 967.

Stratton, G. E. (1997). Investigation of species divergence and reproductive isolation of *Schizocosa stridulans* (Araneae:Lycosidae) from Illinois. *Bull. Br. Arachnol. Soc.* **10**, 313-321.

Stratton, G. E. and Uetz, G. W. (1983). Communication via substrate-coupled stridulation and reproductive isolation in wolf spiders (Aranea: Lycosidae). *Anim. Behav.* **31**, 164-172.

Stratton, G. E. and Uetz, G. W. (1986). The inheritance of courtship behavior and its role as a reproductive isolating mechanism in two species of *Schizocosa* wolf spiders (Araneae Lycosidae). *Evolution* **40**, 129-141.

Suthers, R. A. (1990). Contributions to birdsong from the left and right sides of the intact syrinx. *Nature* **347**, 473-477.

Suthers, R. A. and Zollinger, S. A. (2004). Producing song – the vocal apparatus. *Ann. New York Acad. Sci.* **1016**, 109-129.

Suthers, R. A., Vallet, E., Tanvez, A. and Kreutzer, M. (2004). Bilateral song production in domestic canaries. *J. Neurobiol.* **60**, 381-393.

Taylor, P. W., Roberts, J. A. and Uetz, G. W. (2005). Flexibility in the multi-modal courtship of a wolf spider, *Schizocosa ocreata*. *J. Ethol.* **23**, 71-75.

Uetz, G. W. and Stratton, G. E. (1982). Acoustic communication and reproductive isolation in spiders. In *Spider Communication: Mechanisms and Ecological Significance* (ed. P. N. Witt and J. S. Rovner), pp. 123-129. Princeton (NJ): Princeton University Press.

Uetz, G. W. and Roberts, J. A. (2002). Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain Behav. Evol.* **59**, 222-230.

Virant-Doberlet, M. and Cokl, A. (2004). Vibrational communication in insects. *Neotrop. Entomol.* **33**, 121-134.

von Helversen, D., Balakrishnan, R. and von Helversen, O. (2004). Acoustic communication in a duetting grasshopper: receiver response variability, male strategies and signal design. *Anim. Behav.* **68**, 131-144.