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Sound radiation around a flying fly

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Many insects produce sounds during flight. These acoustic emissions result from the oscillation of the wings in air. To date, most studies have measured the frequency characteristics of flight sounds, leaving other acoustic characteristics—and their possible biological functions—unexplored. Here, using close-range acoustic recording, we describe both the directional radiation pattern and the detailed frequency composition of the sound produced by a tethered flying (*Lucilia sericata*). The flapping wings produce a sound wave consisting of a series of harmonics, the first harmonic occurring around 190 Hz. In the horizontal plane of the fly, the first harmonic shows a dipolelike amplitude distribution whereas the second harmonic shows a monopolelike radiation pattern. The first frequency component is dominant in front of the fly while the second harmonic is dominant at the sides. Sound with a broad frequency content, typical of that produced by wind, is also recorded at the back of the fly. This sound qualifies as pseudo-sound and results from the vortices generated during wing kinematics. Frequency and amplitude features may be used by flies in different behavioral contexts such as sexual communication, competitive communication, or navigation within the environment. © *2005 Acoustical Society of America.* [DOI: 10.1121/1.1932227]

I. INTRODUCTION

Higher flies (Diptera, Brachycera) can emit sound in two different ways: incidentally from the wingbeat during flight, or actively through controlled wing vibrations when resting or walking (Ewing, 1989; Bailey, 1991; Greenfield, 2002). Controlled wing vibrations have been reported in numerous fly families (Sarcophagidae: Thomas, 1950; Chloropidae: Chvála *et al.*, 1974; Muscidae: Ewing, 1977; Tephritidae: Sivinski, 1988; Pscychodidae: Oliveira *et al.*, 2001) and have been studied extensively in *Drosophila* fruit flies (Drosophilidae) where they play a role in courtship behavior (Hall, 1994). In contrast, although the aerodynamics of insect flight have been extensively researched (for a review see Sane, 2003), the sound produced during flight has received less attention. Sotavalta (1947) listed the flight tones of numerous higher fly species, however, his study relied upon his "absolute ear (…) endowed by Nature" making it unrepeatable. Recordings of the tethered flight of *Drosophila melanogaster* made by Bennet-Clark and Ewing (1968), for comparison with the courtship song, were highly replicable but limited to a single position behind the animal.

Higher fly sounds may be of greater interest following a recent biomechanical study that found the antennae of several higher fly representatives responded to sound in a way physically similar to *D. melanogaster* (Robert and Göpfert, 2002). In *D. melanogaster* the male courtship wing vibrations cause air particle displacements that are received by the antennae. The *Drosophila* antenna works as a rotating simple harmonic oscillator, which activates a complex mechanosensory organ, the Johnston's organ (Göpfert and Robert, 2001,

2002). Widespread antennal hearing systems amongst the Brachycera imply the use of sound by more species, and in more contexts, than previously supposed. Robert and Göpfert (2002) suggested that flight sounds could be used by higher flies for flight control and, putatively, close-range echolocation. In some species, such sound could also assist territory defense (e.g., hoverflies—Syrphidae), relative positioning, and mating in swarms (e.g., dance flies—Empididae).

To investigate the possible function of flight sound in higher flies, more information about the radiation pattern and frequency content is needed, particularly in front of the fly where the auditory receivers lie. In insects, sound that is intended for a particular receiver is often directional (Bennet-Clark, 1971; Forrest, 1991; Heller and Krahe, 1994; Michelsen and Elsner, 1999; Michelsen and Fonseca, 2000). Is the sound produced by a flying fly concentrated in a particular direction?

Sotavalta (1947) discusses the reliability of the acoustic method for studying the wingbeat frequency, particularly as many previous authors were apparently confusing the first and the subsequent harmonics. He theorized that the discrepancies were simply due to disagreements in musical notation. Interestingly, Bennet-Clark and Ewing (1968) anecdotally noted that different sounds could be recorded around tethered flying *D. melanogaster*. Their observation presents the possibility of the dominant frequency varying around the fly. This would offer an alternative explanation to Sotavalta's, but has never been confirmed.

Here we analyze in detail the amplitude and frequency composition of the sound field during flight using a typical higher fly, the blowfly *Lucilia sericata* (Calliphoridae). In anechoic and dark conditions, we made high resolution, close-range recordings with miniature pressure-difference microphones revolving around tethered flying individuals. The plane of revolution of the microphones was chosen to

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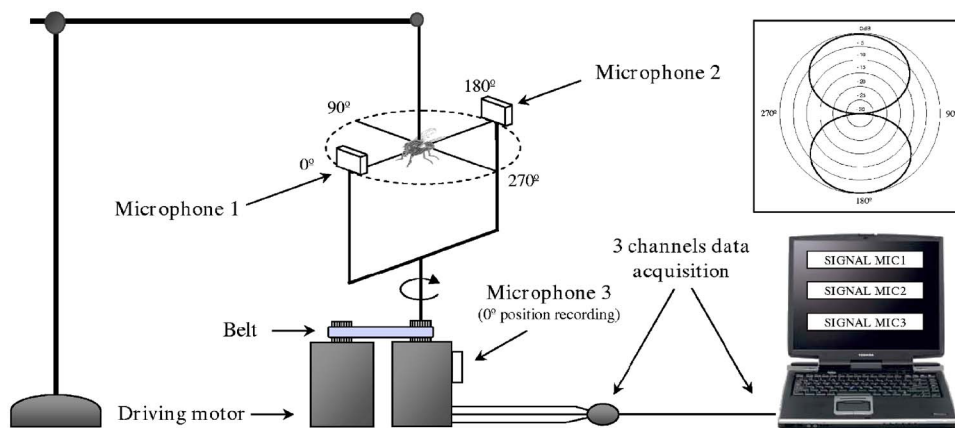
FIG. 1. Diagram of the recording setup and data acquisition system. The two microphones were 4 cm apart and revolved around a tethered fly. The motor was controlled with a second laptop (not shown). The microphone stand was isolated from the vibrations of the motor using a belt. The upper-right box shows the directivity pattern of the microphones (from Knowles™ specifications).

correspond to that of the antennal receiver. We describe both amplitude and frequency variations around the fly and show that the first two frequency bands of the wingbeat do not have the same radiation pattern. In effect the first harmonic dominates in front of the fly whereas the second harmonic is dominant on the sides. Moreover, noise due to vortex formation scrambles the wingbeat sound behind the fly. Such properties may be important for potential auto- or allo-communication.

II. MATERIAL AND METHODS

A. Animals

Male and female blowflies (Diptera, Brachycera, Calliphoridae, *Lucilia sericata*) were taken from laboratory cultures (Insect Ecology and Veterinary Parasitology Laboratory, University of Bristol). Prior to use, animals were maintained in plastic cages ($0.53 \times 0.22 \times 0.22$ m^3) and fed with sugar and water. Flies were anaesthetized with CO_2 and tethered with small piece of rigid card (surface ≈ 20 mm^2) fixed dorsally to the thorax with wax; the flies were then allowed at least 2 h to recover. Eight males and eight females whose free-flight behavior in the cage was unaffected by the tether and that flew consistently for more than a minute were selected.

B. Recording procedure

All recordings were carried out in the center of a sound-proof room where the ambient temperature was kept at 25 °C and the relative humidity at 30%. To avoid any visual stimuli that could have modified the flight pattern, experiments were carried out in the dark, with the computer displays being screened by black fabric. The ambient noise level in the center of the setup was 31.3 dB SPL (*re* 20 μPa).

The recording setup consisted of a fly holder positioned between two miniature pressure-difference microphones, Knowles NR-3158 (Knowles Electronics Co, West Sussex, UK), that work as particle velocity receptors (Göpfert and Robert, 2002). The microphones were mounted on a rotating fork-shaped stand (Fig. 1). The vertical axle of this stand was belt driven, by a PC laptop controlled motor (Bipolar Stepper Motor, Milford Instruments, Leeds, UK). The belt mechanically isolated the stand and the acoustic recordings from the motors vibrations. The two microphones recorded the sound

field from opposite sides of the fly to verify and double the data per sample. The microphones used were highly directional with a typical figure-of-eight directivity pattern (maximal input for a sound source angle at 0° or 180° and minimal input at 90° or 270°) (Fig. 1 inset) and they were therefore made to face the fly throughout each rotation. The microphone dimensions were $4.00 \times 5.59 \times 2.28$ mm^3 and their frequency response was flat between 0.1 and 2 kHz.

The revolution of the stand had a period 1.194 ± 0.012 s ($n=200$) indicating an error of 1%. A brief sound marking one complete rotation (duration=0.1 s, frequency=2.5 kHz) was triggered when the rotary stand crossed the zero degree position, i.e., just in front of the fly's head. The 2.5-kHz frequency was chosen as it would not interfere with the fly's flight sound. The reference sound was recorded using a Vivanco EM-216 microphone (Ahrensburg, Germany). To reduce the effect of irregular flight sound emissions during acquisition, each individual was recorded for ten revolutions of the stand, generating 320 sound files (16 individuals $\times$ 10 revolutions $\times$ 2 microphones).

The three microphones were connected to a second PC laptop through custom-made amplifiers and a four-channel Maya 44 USB audio interface (Audiotrak, San Jose, USA). Sounds were digitized at a sampling rate of 44.1 kHz and at 16-bit resolution using the multi-channel recording software Sonar 2.2 (http://www.cakewalk.com). They were stored as .wav files without data compression.

The distance between microphones was 4 cm and the fly was positioned directly in between. As the distance between the fly and the microphones was much smaller than the flight sound wavelength ($r/\lambda \ll 1$, with r=distance from the source, λ=wavelength), the microphones were in the acoustic near field. Any reflection and diffraction by surrounding setup is considered negligible since the width of the stand (0.01 m) was much smaller than the wavelength of the sound recorded (between 3.47 and 0.69 m for sounds between 100 and 500 Hz). No other object capable of interfering with the recordings was present in the surrounding sound field.

C. Amplitude analysis

Initial spectrographic analysis using the software package SYNTANA (Aubin, 1994) showed that the continuous wingbeat sound consisted of a harmonic series. The first ($F1$;

around 200 Hz) and second harmonic ($F2$; around 400 Hz) alternately contributed the most energy. To study the amplitude variations of the first and second harmonics two band-pass filters were independently applied. The filters were calculated by means of a fast Fourier transform (FFT) with a window of 4096 points enabling a frequency precision of 1.22 Hz. The first filter kept frequencies between 100 and 300 Hz and the second filter kept frequencies between 300 and 500 Hz.

In order to compensate for the 1% error in the revolution period and to obtain files with an identical number of points (5970) despite different durations, signals were under-sampled at different frequencies (5000 ± 48 Hz, $n=200$) using the digital audio editor software Goldwave 5.6 (http://www.goldwave.com). This process did not affect the large amplitude modulations that we wanted to analyze.

Large amplitude modulations around the fly were estimated from the signal envelope. Envelopes were generated using the Hilbert transform (Mbu-Myamsi *et al.*, 1994). We normalized the envelopes to obtain values between 0 and 1. Ten first harmonic $F1$ and ten second harmonic $F2$ envelopes were calculated from both microphones and averaged for each individual. This resulted in four averaged envelopes per individual. To facilitate visual comparison, normalized envelopes were converted to an intensity decibel (dB) scale $[a_i(\mathrm{dB}) = 10 \log a_i]$.

D. Frequency analysis

To determine the dominant frequency around the fly, sound files were undersampled to the same sampling frequency (5000 Hz) and subjected to successive Fourier transforms (FTs) using a Hanning window of 1024 points (=0.2 s). This frame length led to a frequency resolution of 4 Hz. Ninety overlapping FTs were calculated per rotation enabling a spatial resolution of 4°.

Since the harmonics could be considered as discrete variables, we calculated the median instead of the mean of the ten frequency modulations obtained for each individual and calculated the male and female average frequency from this.

E. Control

The accuracy of the recording setup was estimated using a small unbaffled loudspeaker (Wharfedale AKI-1200, diameter 1.5 cm, impedance 32 Ω, 20–20 000 Hz) firmly clamped in place of the fly. The loudspeaker was successively fed with continuous sinusoidal signals of 200 and 400 Hz generated by SYNTANA. At these frequencies, an opened loudspeaker acts as a dipole sound source, i.e., radiating sound with a maxima along the 0° and 180° directions, and minima along the 90° and 270° directions (Russell *et al.*, 1999). Amplitude and frequency modulations of the 200- and 400-Hz signals were then estimated using the same process as described for the flies' acoustic emissions above.

F. Wing morphometry

Thoracic width measurements were made between the left and right wing articulations for eight male and eight female *L. sericata* using a binocular dissecting Wild M5 Microscope and an eyepiece graticule. The wings were cut and scanned at 800 dpi resolution and wing length and area were then measured using the software tpsDIG32 version 1.40 (Rohlf, 2004).

G. Statistical analysis

Sound data from the two microphones were aligned to 0° and the envelopes and dominant frequency values were compared using Spearman's rank correlation coefficient and Mann-Whitney test. The envelopes were considered as vectors, with vector length (modulus) corresponding to amplitude and vector angle (argument) corresponding to the microphones position around the fly. Amplitude directivity was estimated from the mean vector (L, θ) and circular standard deviation (ν) as (Fischer, 1995):

$$L = \frac{\sqrt{\left(\sum_{i=1}^{i=n} a_i \cos \alpha_i\right)^2 + \left(\sum_{i=1}^{i=n} a_i \sin \alpha_i\right)^2}}{n}, \text{ with } 0 < L < 1,$$

$$\theta = \begin{cases} \tan^{-1}\left(\dfrac{\sum_{i=1}^{i=n} \sin \alpha_i}{\sum_{i=1}^{i=n} \cos \alpha_i}\right) & \text{if } \sum_{i=1}^{i=n} \sin \alpha_i > 0, \sum_{i=1}^{i=n} \cos \alpha_i > 0, \\[6pt] 180 + \tan^{-1}\left(\dfrac{\sum_{i=1}^{i=n} \sin \alpha_i}{\sum_{i=1}^{i=n} \cos \alpha_i}\right) & \text{if } \sum_{i=1}^{i=n} \cos \alpha_i < 0, \\[6pt] 360 + \tan^{-1}\left(\dfrac{\sum_{i=1}^{i=n} \sin \alpha_i}{\sum_{i=1}^{i=n} \cos \alpha_i}\right) & \text{if } \sum_{i=1}^{i=n} \sin \alpha_i < 0, \sum_{i=1}^{i=n} \cos \alpha_i > 0, \end{cases}$$

$$\nu = \frac{180}{\pi}\sqrt{2(1-L)}, \quad \text{with } 0 < \nu < 81.03°.$$

Since the loudspeaker showed a centrally symmetrical amplitude distribution (i.e., bimodal), the vector of the resulting mean would be around zero and no mean angle could be determined. Following Fischer (1995), the mean vector and angle were calculated applying the following correction $\alpha_i \rightarrow 2\alpha_i$ when $2\alpha_i < 360°$ and $\alpha_i \rightarrow 2\alpha_i - 360°$ when $2\alpha_i \geqslant 360°$.

Wing morphometric data were compared using the Mann-Whitney test. Statistics tests followed Sokal and Rohlf (1995) and were computed with SPSS 11.0 software (SPSS Inc., Chicago, IL).

III. RESULTS

A. Control

Control recordings and analyses were done with a small unbaffled loudspeaker and the amplitude envelopes for both sine waves (200 and 400 Hz) showed a typical figure-eight pattern. With the minimum amplitude levels at 90° and 270° and an amplitude difference of about 2 dB between the back and the front of the loudspeaker, the mean direction was 0° (Fig. 2). Such a polar amplitude profile is typical of unbaffled loudspeakers. Small variations revealed that recordings at 200 Hz were noisier than at 400 Hz but these were not sufficient to affect the large amplitude modulations. The amplitude envelopes did not differ between the two micro-
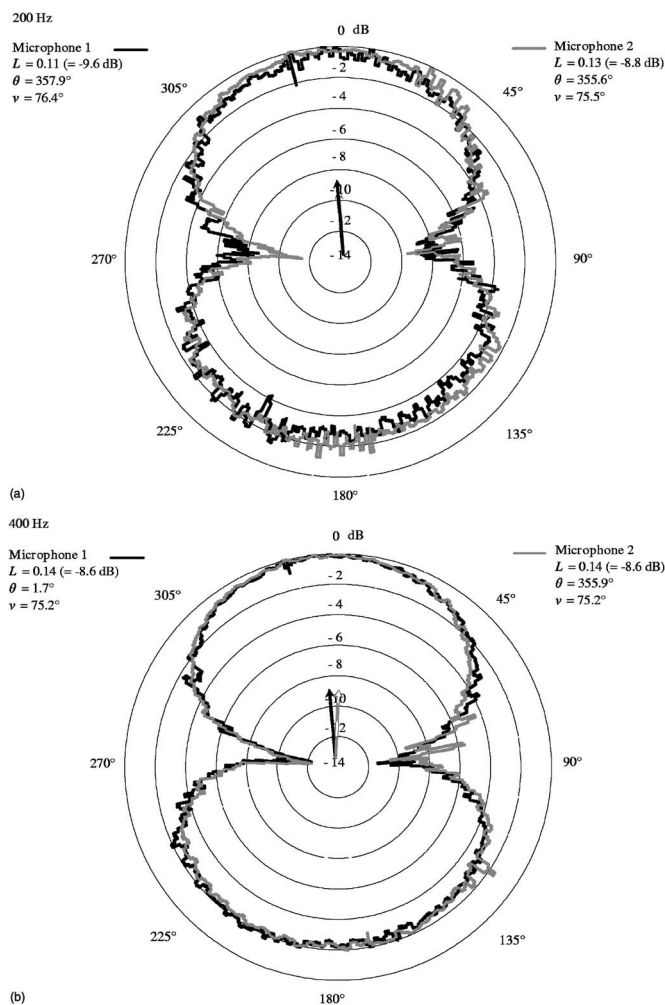
FIG. 2. Control of amplitude analysis: amplitude variations around a small unbaffled loudspeaker emitting successively a 200-Hz (a) and a 400-Hz (b) sine wave. The loudspeaker faced the 0° position. For each microphone, the amplitude directivity is characterized by mean vector length (L), mean vector direction (θ), and circular standard deviation (ν).

phones ($P < 0.0001$ in all cases, Spearman correlation). The average amplitude difference between the two microphones was 0.14 dB at 200 Hz and 0.04 dB at 400 Hz. Analysis of the dominant frequency indicated a slight frequency shift; 193.5 ± 2.2 and 385.2 ± 0.9 Hz for microphone 1, 193.4 ± 2.6 and 385.1 ± 1.4 Hz for microphone 2 (Fig. 3). The loudspeakers were forcibly very small (diameter=1.5 cm) to permit the microphone movement. The frequency error occurred due to the high impedance (32 Ω) of the small loudspeaker, which therefore required high broadcasting levels to obtain an acceptable signal. Two larger loudspeakers with static microphones confirmed that this was the case. Frequency analysis did not show any significant differences between the two microphones (absolute difference between microphones 1 and 2: 2.58 Hz at 200 Hz, 0.58 Hz at 400 Hz, $P > 0.5$ in both cases, Mann-Whitney test). Microphones specifications could be then considered as similar.

B. Amplitude analysis

The spectrogram depicted in Fig. 4 illustrates a typical sound recorded around a flying *L. sericata*. The amplitude of
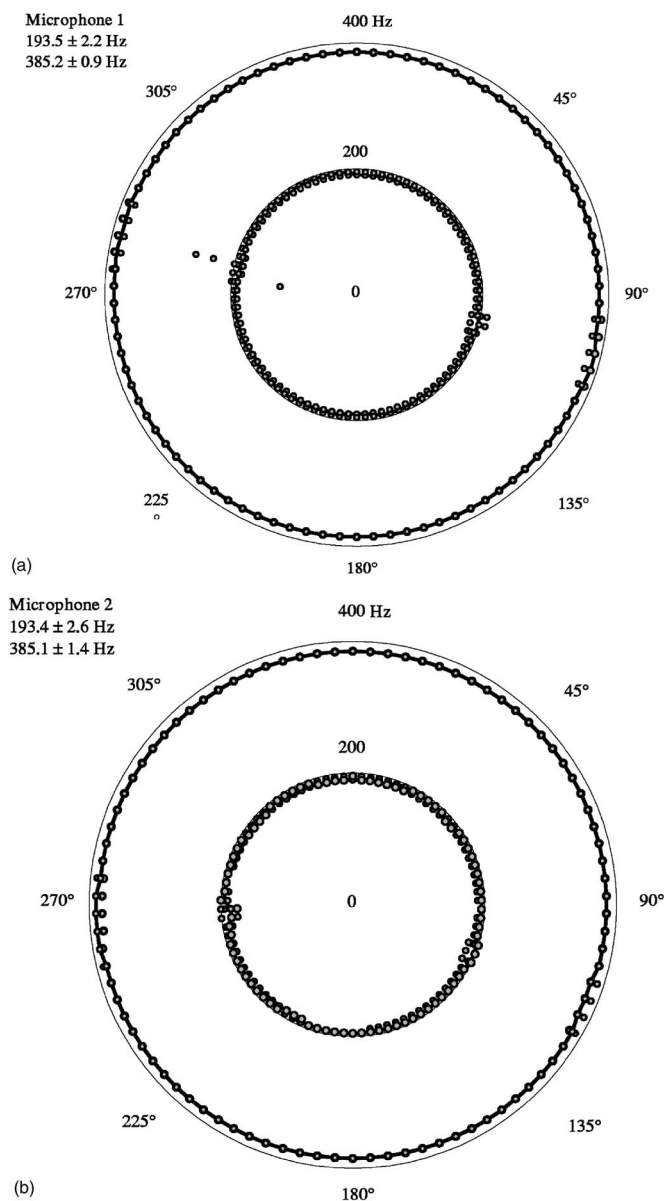

FIG. 3. Control of frequency analysis for the two microphones (a, b): measuring with 4° precision the frequency of 200- and 400-Hz sine waves. The points represent the dominant frequency every 4° during one revolution around the loudspeaker. Ten revolutions were analyzed. Low variability in the results led to point superposition. Black lines correspond to the median of the points.

the signal is modulated around the fly, with the maximum occurring around 180°. Amplitude modulations for the first ($F1$) and second harmonic ($F2$) obtained by signal envelope computation are shown in Fig. 5. In all cases, the mean vector modulus (L) was very small (<0.15), indicating a high level of dispersion. This was confirmed by the high values of angular dispersion (ν) around 80° for a scale ranging from 0° to 81°. Mean vector arguments were concentrated behind the flies ($201° < \theta < 297°$), except for $F1$ produced by males where values were around 300°. Low L and ν values, such as those calculated for the male $F1$, however, indicate the mean vector argument is not very accurate.

The radiation pattern of $F1$ was a figure-eight, with the lowest amplitude values at 100° and 260° and the highest at 0° and 180°. Males and females produced similar overall
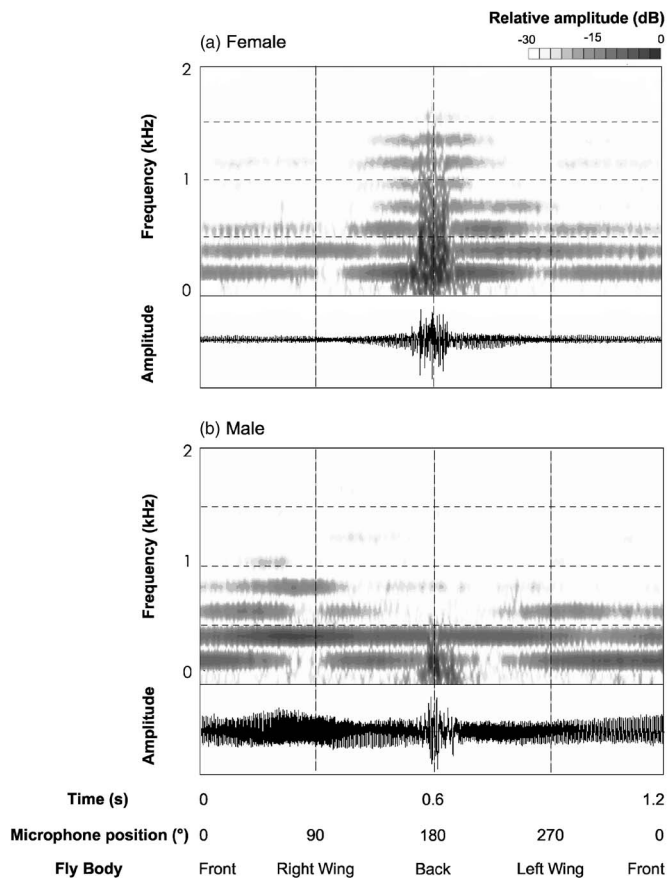
FIG. 4. Spectrogram of a typical sound recorded around *Lucilia sericata* female (a) and male (b). Fast Fourier transform window length=1024 points, frequency resolution=4.9 Hz, overlap=98%, Hanning window. 1 gray scale=2.5 dB.

patterns although the correlation between them for $F1$ was lower $(0.69, 0.71, P < 0.0001)$ than between the two microphones $(0.95, 0.97, P < 0.0001)$, indicating some differences between the two sexes. Indeed males produced louder $F1$ values than females (difference male-female: microphone 1 =3.0 dB, microphone 2=2.9 dB) and this difference was greater in the front (difference male-female between 270° and 90°: microphone 1=4.1 dB, microphone 2=4.2 dB) than the back (difference male-female between 90° and 270°: microphone 1=1.9 dB, microphone 2=1.6 dB).

The radiation of $F2$ exhibited a more circular pattern, with points of higher amplitude at approximately 100° and 260° (Fig. 5). The radiation differences of $F1$ and $F2$ are confirmed by the low correlation coefficient for females $(0.61, 0.77, P < 0.0001)$ and even negative correlation for males $(-0.55, -0.50, P < 0.0001)$. The correlation coefficients for $F2$ between the males and females were all significant $(0.62, 0.55, P < 0.0001)$ but lower than that of the two microphones $(0.93, 0.97, P < 0.0001)$. Again, the males were louder (microphone 1=1.3 dB, microphone 2=1.8 dB) with the greatest difference being in the front (microphone 1 =2.15 dB, microphone 2=2.5 dB) compared to the back (microphone 1=0.5 dB, microphone 2=1.1 dB).

C. Frequency analysis

When flying, *L. sericata* produced a series of harmonics the first of which ($F1$) was around 200 Hz and the second

one ($F2$) also being consistently intense enough for recording. Male $F1$ and $F2$ values were respectively 192±30 and 390±24 Hz for the microphone 1 and 189±22 and 391±16 Hz for microphone 2. Female $F1$ and $F2$ values were respectively 193±18 and 377±8 Hz for the microphone 1 and 190±14 Hz and 377±7 Hz for microphone 2. $F1$ and $F2$ values were not different between microphones 1 and 2 ($P > 0.5$ in all cases, Mann-Whitney test). $F1$ values were not significantly different between males and females ($U=3152.5$, $P > 0.05$, microphone 1; $U=29295.5$, $P > 0.05$, microphone 2; Mann-Whitney test) but there was a significant difference of about 13 Hz between males and females for $F2$ values ($U=1605$, $P < 0.0001$, microphone 1; $U =1841$, $P < 0.0001$, microphone 2; Mann-Whitney test).

Spectrograms of a typical recording around a flying individual clearly show that the relative energies of $F1$ and $F2$ were modulated around the fly (Fig. 2). $F1$ was of highest energy (i.e., dominant) at around 0°, but disappeared almost entirely between 100° and 260° where $F2$ increased to become dominant instead. In addition, an intense broadband noise partly covered both $F1$ and $F2$ at 180°.

To confirm these observations, we determined the dominant frequency at different positions around the fly (Fig. 6). The results from both microphones were similar ($r=0.892$ for male, $r=0.878$ for female, $P < 0.0001$ in both cases, Spearman correlation) and the male and female frequency patterns were not significantly different ($r=0.889$ for microphone 1, $r=0.891$ for microphone 2, $P < 0.0001$ in both cases, Spearman correlation). $F1$ was most frequently dominant in the front ([305°–45°]) and in the back ([125°–225°]) whereas $F2$ was dominant on both sides ([45°–125°], [225°–305°]). A single Fourier transform at 0°, 90°, 180°, and 270° for one individual further illustrates this phenomenon (Fig. 7). At the rear of the fly, the harmonic series is partly covered by airflow noise, generated by the fly, ranging from 0 to around 800 Hz.

D. Wing morphometry

Thorax width between left and right wing articulations was 3.0±0.2 mm for eight males and 3.0±0.1 mm for eight females. There were no differences between the male and female inter-wing distance ($U=27$, $P > 0.05$, Mann-Whitney test). Male wing area was 13.58±1.70 mm^2 (left) and 13.35±1.38 mm^2 (right). Female wing area was 16.73±0.97 mm^2 (left) and 16.25±0.91 mm^2 (right). There were no differences between left and right wings ($U=28$, $P > 0.5$ for males; $U=21$, $P > 0.5$ for females; Mann-Whitney test). Male wings were smaller than female wings (left wing: $U=2$, $P < 0.005$; right wing: $U=0$, $P < 0.001$; Mann-Whitney test).

IV. DISCUSSION

A. Sound and flight

The flight sound of *L. sericata* is ineffectually directed and is characterized by a series of harmonics with a noise recorded behind the fly. Typically, the first harmonic was dominant in front and the second harmonic was dominant at the sides. The first harmonic showed a dipolelike pattern,
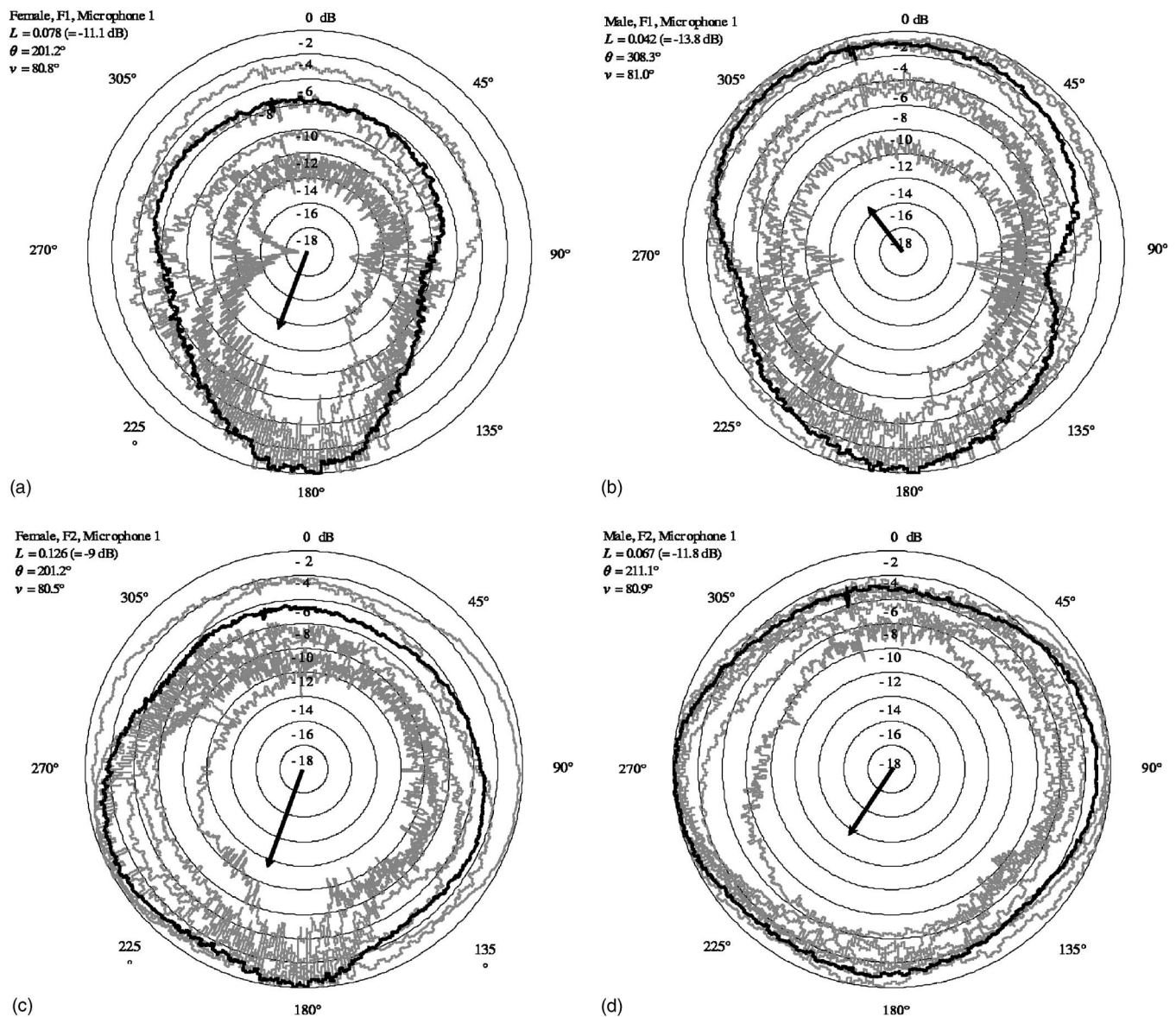
FIG. 5. Amplitude variations of first ($F1$) and second harmonic ($F2$) bands around flying tethered females (a, c) and males (b, d). Gray lines: mean of ten revolution around single individuals. Black lines: mean of the gray lines. Descriptive parameters as in Fig. 2. Data is shown for one microphone only but was typical of both.

whereas the second harmonic exhibits a more rounded envelope like a monopole.

Our finding that the dominant frequency switches between the first and second harmonic frequency at different positions around the fly could explain why earlier observers could not agree upon the flight tone of certain insect species (Sotavalta, 1947). This phenomenon may occur because the wing motion is not a simple vertical oscillation but includes velocity variations, wing deformations, and rotations (Ellington, 1984; Ennos, 1989; Lehmann and Dickinson, 1998; Dudley, 2000). Indeed, Fletcher (1992) points out that modeling the wing as a simple vibrating disc (dipole) is only moderately satisfactory. Bennet-Clark and Ewing (1968), however, showed that the flight sound waveform of *D. melanogaster* follows a similar time course to the wing-tip velocity. If we consider that the observed angle, motion, and velocity of the wing tips are dependent upon the viewer's

position around the fly, this could explain how the dominant frequency also varies.

In the rear of the fly the harmonics were masked by a loud sound that had a broad unstructured frequency content and was analogous to recordings of airflows. This nonperiodic waveform may have been caused by vortices, which, having been formed and shed by the wings, trail behind a flying insect (Grodnitsky and Morozov, 1993; Brodsky, 1994; Dickinson and Götz, 1996; Ellington *et al.*, 1996; Dudley, 2000). Since this "sound" results from fluctuating movements of the airflow rather than periodic air vibrations, it should be more accurately described as "pseudo-sound" (Lighthill, 1962). Our recordings suggest that females produced more pseudo-sound than males. These differences were unlikely to be caused by body-size differences since thorax length measurements were similar in both sexes. Male flies had smaller wings however (wing area around 13 mm^2

400 Hz

305°   45°

200

270°   90°

0

225°   135°

(a)

180°

Male Microphone 1

400 Hz

305°   45°

200

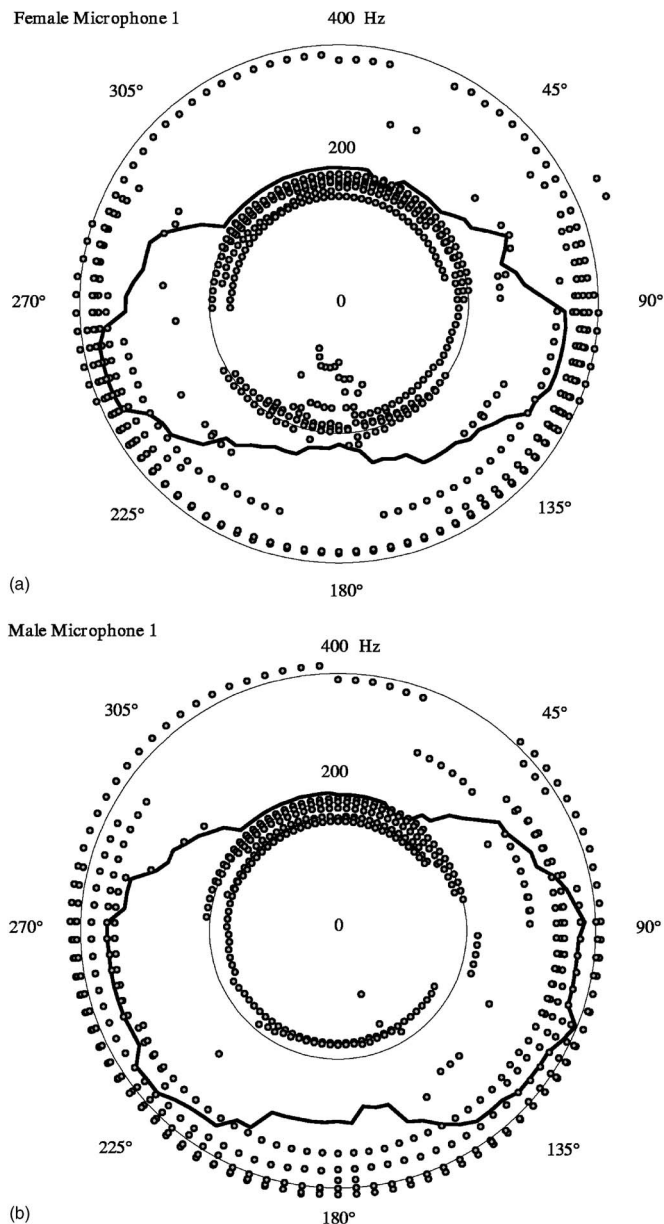270°   90°

0

225°   135°

(b)

180°

FIG. 6. Measuring with 4° precision of the dominant frequency band in female (a) and male (b). Each point represents the median of ten measures corresponding to ten revolutions around a single individual. Lines correspond to the mean of the points. Data is shown for one microphone only but was typical of both.

for males and 16 mm^2 for females), which might displace less air and therefore generate less intense wake vortices than females. One would expect any differences in the amplitude of the wingstroke to have a similar effect.

Interestingly Bennet-Clark and Ewing (1968) did not detect any such pseudo-sound when recording from behind a flying *D. melanogaster*. This may reflect differences in the wake dynamics of two distinct fly species and in the relative distances of recording. The work of Lighthill (1962) suggests that flight sound and pseudo-sound will dissipate differently. In the far field, sound pressure and sound velocity decrease inversely with the distance from the source ($1/r$) whereas pseudo-sound amplitude decreases with at least the inverse square ($1/r^2$) (Lighthill, 1962). In the near field pseudo-sound attenuation is unknown but sound pressure and sound

velocity are thought to decrease by $1/r$ and $1/r^2$ respectively for a monopole, and by $1/r^2$ and $1/r^3$ respectively for a dipole (Bennet-Clark, 1998). In principle, then, further from the fly the harmonic series will outlast the pseudo-sound and should therefore be recorded instead.

The harmonic series and/or the pseudo-sound could potentially encode information relevant to a fly. Our results suggest, however, that the flight sounds of a fly are not radiated very efficiently. For efficient sound production, the source size must be higher than $\frac{1}{6}$ (monopole) or $\frac{1}{4}$ (dipole) of the wavelength (Bennet-Clark, 1998). Hence the size (or the mass) of the emitter is often inversely proportional to the frequency of the sound produced (Bennet-Clark, 1998; Fletcher, 2004). In this case, the wings of *L. sericata* are much smaller than the wavelength of the sound they produce (around 1.8 m).

Some insects solve the frequency-scale problem using external secondary structures, such as a baffle, which may also help direct the signal (e.g., tree-crickets: Forrest, 1991). A flying fly lacks any obvious external baffle and three of the mean vector analyses indicate that the flight sound of *L. sericata* is only weakly directed to around 200°. Unlike the envelopes and mean vectors computed for the fly, however, the control does not demonstrate this sagittal asymmetry. This suggests that an asymmetry in the animal preparation or in the experimental environment may have influenced the fly's flight. The rearward concentration of sound energy was probably due to the pseudo-sound at the back. The lesser pseudo-sound recorded behind male flies could explain why the energy of the males' first harmonic is weakly directed to around 300°. This would suggest that in the absence of pseudo-sound the energy of the first harmonic is concentrated forwards whereas the energy of the second harmonic remains angled backwards.

B. Flight sounds and hearing

Robert and Göpfert (2002) suggest that antennal sound reception might be possible in several families of higher flies. The use of flight sounds for communication by members of the Brachycera, however, has never been reported. In static *D. melanogaster* the resonant frequency range of the antenna peaks at around 420 Hz (Robert and Göpfert, 2002). Courtship song detection is usually used to explain this antennal tuning which interestingly also coincides with the acoustic wingbeat frequency (Bennet-Clark and Ewing, 1968). Potentially acoustic sensitivity to the wingbeat could present a sensory problem during flight. Indeed, animals that produce loud and continuous sounds risk deafening themselves by overworking their acoustic sensory organs. "Ear" protection can be achieved by actively modifying the properties of the hearing organ as an Australian cicada does by folding its tympanic membrane while calling (Henning *et al.*, 1990). Göpfert and Robert (2002) showed that in *D. melanogaster* as the sound intensity increases, the resonant frequency of the antenna shifts, so that its acoustic sensitivity decreases. Our results allude to a passive protective system. The antennae of *L. sericata* are in a position where the acoustic energy of the sound field is concentrated on the first
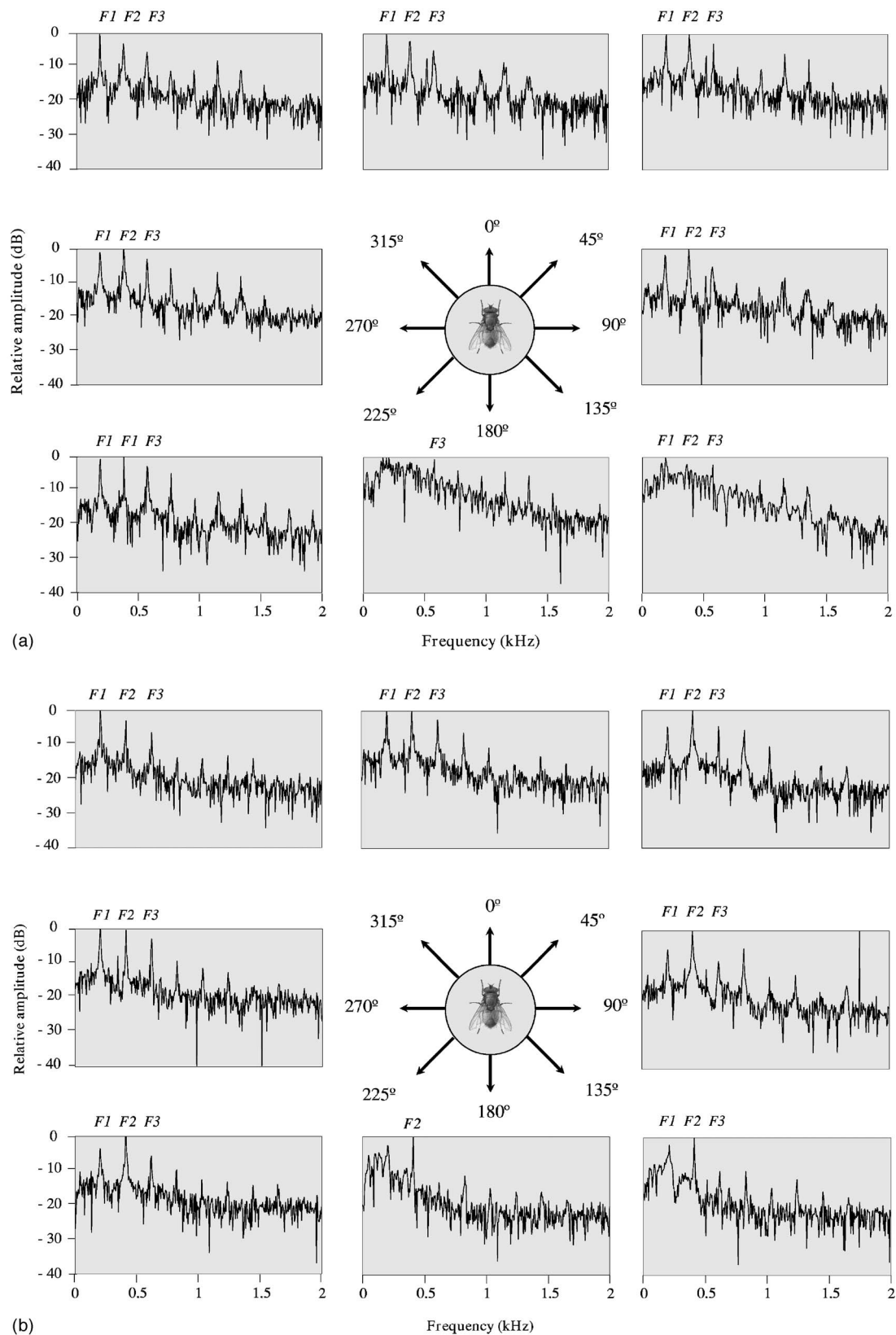
FIG. 7. Frequency spectrum of a recording around *Lucilia sericata* female (a) and male (b) at 45° positions. *F*1, *F*2, and *F*3 localize, respectively, the first harmonic, second, and third harmonic bands. Characters in bold indicate the dominant frequency. Fourier transform window length=1024 points, frequency resolution=4.9 Hz, Hanning window. Data is shown for one microphone only but was typical of both.

harmonic, around 200 Hz. If tuned to the second harmonic rather than to the first frequency band, *L. sericata* would be partially protected against its own sound, but would still be able to detect the sound produced on the sides by congeners.

If *L. sericata* can receive sound during flight without damage, it could exploit self-generated and conspecific flight sounds for auto- and allo-communication, respectively. As explained previously, the flight sounds of *L. sericata* are not radiated very efficiently and therefore are more likely to function in short-range communication. In the plane we studied, there was no evidence that the sound field was directed towards a particular receiver. The position of the receiver may still be important however, as the frequency content is variable around the fly.

In order to fully estimate how sound might be used during flight, the results we obtained would have to be completed by an analysis in three dimensions and analysis of the antennal reception mechanism. Behavioral experiments testing the potential role of such particular sound emissions should also be undertaken.

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