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Digger wasp against crickets.
II. An airborne signal produced by a running predator

Werner Gnatzy[1]* and Günter Kämper[2,]**

[1] Zoologisches Institut der J.W. Goethe-Universität, Siesmayerstr. 70, D-6000 Frankfurt am Main 11, Federal Republic of Germany
[2] Max Planck-Institut für Verhaltensphysiologie, Abteilung Huber, D-8131 Seewiesen, Federal Republic of Germany

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Summary. Females of the digger wasp *Liris niger* Fabr. hunt crickets to provide food for their offspring by running with high velocity on the ground (>20–50 cm/s). Crickets are able to detect the running wasps by the air particle movement generated by the predator. We measured signals produced by running wasps using a microphone sensitive to air particle velocity. The wasps generated single air puffs with peak air particle velocities of 1–2 cm/s measured close to the running wasp. We measured frequency spectra of the signals containing only components below 50 Hz, with increasing intensities towards lower frequencies, especially below 10 Hz.

We measured the air particle movement generated by artificially moved wasps, crickets or a styrofoam dummy of similar size to investigate the effect of velocity and shape of the moving object upon the composition of the signal. The velocity of movement appeared to be important for the intensity and frequency composition of the air particle movement. The shape of the moved body had an influence on the intensity but only little effect on the frequency spectrum. Measurements with a thermistor anemometer showed that a moving object caused air currents lasting longer than 100 ms after passing or approaching the probe. The air particle movements generated by hunting wasps are entirely sufficient with respect to intensity and frequency range to be registered by the filiform hair sensilla upon the cerci of crickets.

Key words: Air particle movement – *Liris niger* – *Acheta domesticus* – Insect

Introduction

Many insects show defensive behaviors. Responses of prey animals to stimuli produced by predators range from freezing and immediate escape attempts to complex behavioral sequences involving special defensive postures (Steiner 1968; Edmunds 1972; Markl and Tautz 1975; Sandow and Bailey 1978). There are only a few examples where airborne stimuli produced by a predator eliciting such behavioral responses have been measured (Tautz 1977; Tautz and Markl 1978; Camhi et al. 1978; Plummer and Camhi 1981).

We studied the interactions between females of the sphecoid wasp *Liris niger* (which inhabits arid zones of Southern France) and crickets. The females of *L. niger* hunt and paralyze exclusively crickets, both nymphs and adults, preferably of the species *Acheta domesticus* (Gnatzy et al. 1989). The prey is brought into a nest burrowed previously by the wasp, where it attaches a single egg to the cricket. Later the developing larva uses the paralyzed cricket for food (Steiner 1968).

The typical strategy of *L. niger* for hunting crickets is not by flying but rather by running very fast on the ground. Approaches of hunting wasps and their attacks elicit characteristic behavioral reactions in the crickets. They either respond with escape or defensive reactions. A typical defensive reaction is a 'head-stand', i.e. the crickets suddenly raise their abdomen from a resting position. Usually a 'head-stand' is triggered before any direct contact occurs between the animals, after the hunting wasp comes within a radius of 1 to 3 cm as measured from the rear end of the cricket abdomen. The running speed of the wasp has to be faster than about 20 cm/s (Gnatzy and Heußlein 1986) or the cricket exhibits no reaction until there is direct contact with the wasp. 'Head-stand' behavior is triggered by input from filiform hairs on the cerci of the crickets (Gnatzy and Heußlein 1986); these sensilla are mechanoreceptors (Gnatzy and Tautz 1980) that react very sensitively to weak air currents (Kanou and Shimozawa 1984).

In the present study we found that a running predator as small as *L. niger* produces single air puffs which are suited with respect to peak air particle velocity and spectral composition to be detected by the cercal filiform hairs.

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* To whom offprint requests should be sent
** *Present address:* Abteilung für Vergleichende Neurobiologie, Universität Ulm, Postfach 4066, D-7900 Ulm, Federal Republic of Germany

Materials and methods

We used females of *Liris niger* Fabr. (body length 8–15 mm), collected in Southern France near Nimes and Orange. In the laboratory they were fed with honey and water ad libitum and supplied with *Acheta domesticus* L. (nymphs and adults) as provisions for their brood (for additional details on breeding *Liris* see Gnatzy and Heußlein 1986).

Signal recordings from freely moving wasps. Air particle movements caused by running wasps during their hunt for crickets were recorded with a particle-velocity microphone (modified after Bennet-Clark 1984). This microphone is a pressure-gradient receiver the signal of which is electronically transformed to be proportional to air particle velocity. The microphone amplifier also described by Bennet-Clark was modified in order to shift the frequency range from originally 100–5000 Hz to 5–500 Hz (±5 dB, phase lead relative to particle velocity changes from 80° at 5 Hz to 10° at 500 Hz). Frequency range and phase shift were calibrated using a vibration box (following the description of Tautz 1979). From these data we calculated the absolute values of air particle velocity for frequencies in the range 7–10 Hz.

Wasps were running in a box (area 30 × 6 cm, height 25 cm) with walls made of gauze; the floor was covered with sand. We inserted the microphone through a hole in the wall and placed it directly above the sand (electret membrane vertical, center of membrane 5 mm above the sand surface). The running course of the wasps with respect to the position of the microphone was observed directly and drawn; the microphone signals were stored on a FM tape recorder (Racal). The temperature within the box was kept at ca. 30° C.

Recordings of signals produced experimentally by moving dead specimens and dummies. Air particle movement caused by experimentally moved wasps, crickets and a styrofoam dummy (square, 16 × 6 × 10 mm, oscillated along its long axis) were measured with the microphone described above and with a thermistor anemometer (thermistor BC 32 L1) the output of which is proportional to air particle velocity to frequencies below 5 Hz down to 0 Hz (equivalent to constant wind). For principal reasons (hot air surrounding the thermistor) the anemometer can not record the higher frequency components of signals like air-puffs, as does the microphone.

Freshly killed wasps and crickets were air-dried in their normal standing posture and glued to the tip of a glass pipette, which was attached to the pen holder of an XY-plotter (Bryans 26700). By application of a rampform signal to the plotter input the specimens were moved at defined velocities of 1–120 cm/s past the microphone or thermistor close to sandy ground. The electret membrane of the microphone was adjusted vertically and the movement direction of the specimen was perpendicular to the plane of the membrane. The recorded signals were averaged (64 sweeps) to increase the signal-to-noise ratio by a Nicolet Signal Analyser (Model 1074).

Spectral analysis. Spectral analysis of the measured signals was performed using the SPARTA program of a DEC PDP 11/40 computer (Digital Equipment). All spectra given in this paper are power

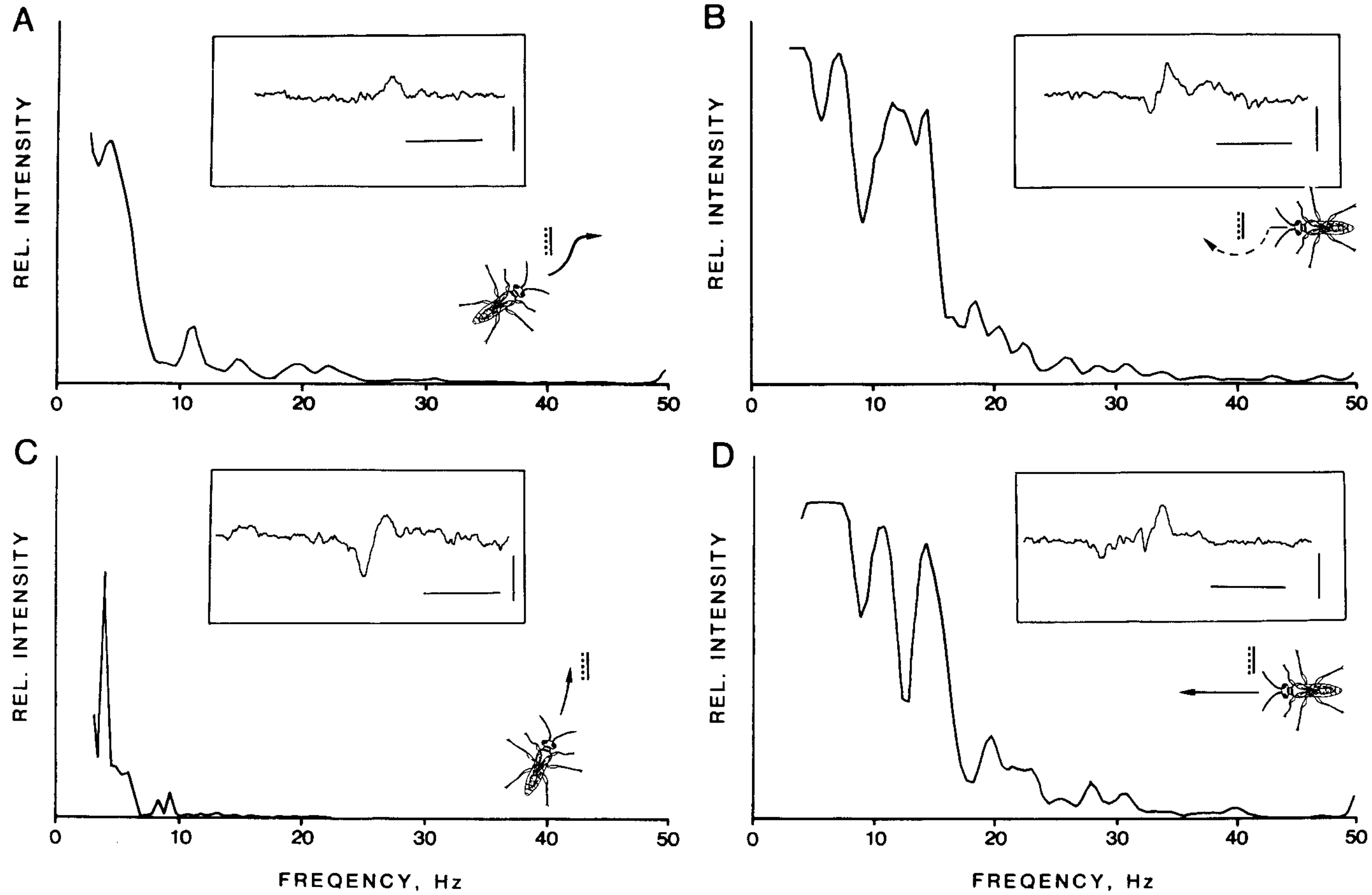

Fig. 1 A–D. Frequency spectra of 4 microphone signals recorded from freely moving running wasps. *Upper insets*: microphone signal, cal. 500 ms. 200 mV (corresponding to a particle velocity of about 1.5–2 cm/s). *Lower insets*: running course of the wasps relative to the microphone probe (dotted line: grid electrode, parallel continuous line: electret membrane; diameter of the electret: ca. 6 mm); in **B** it was uncertain whether the animal went around the probe during the recording (dashed line)

spectra of air particle velocity. Due to the drop in sensitivity of the microphone at low frequencies, spectra resulting from such recordings are shown only for frequencies above 4 Hz.

Results

Recordings from freely moving wasps

With the microphone near the ground of a box in which *L. niger* females were running, we recorded airborne vibrations produced by wasps which approached the probe and passed nearby it (Fig. 1 A–D, insets). The time course of the signals varied, depending on the running path and the size and speed of the animals.

Monophasic as well as biphasic pulses were recorded (compare Fig. 1 A and C). We never recorded periodic oscillations. Spectral analysis performed with pulses occurring during single approachs (Fig. 1 A–D) showed intensity peaks only at frequencies below 50 Hz, with the main peaks below 20 Hz. The signals correspond to air particle velocities of about 1–2 cm/s at the electret membrane of the microphone (calculated according to the microphone and amplifier characteristics at a frequency of 7–10 Hz).

Air currents generated by the movement of fixed specimens and dummies

With a living wasp as stimulus source we did not find series of periodic oscillations that were, for instance, related to leg movements during running. Apparently the recorded air movement was generated by the body of the wasp and not by its legs. For a more detailed measurement of the effects of body length and velocity of motion on the recorded signals we used fixed animals and styrofoam dummies.

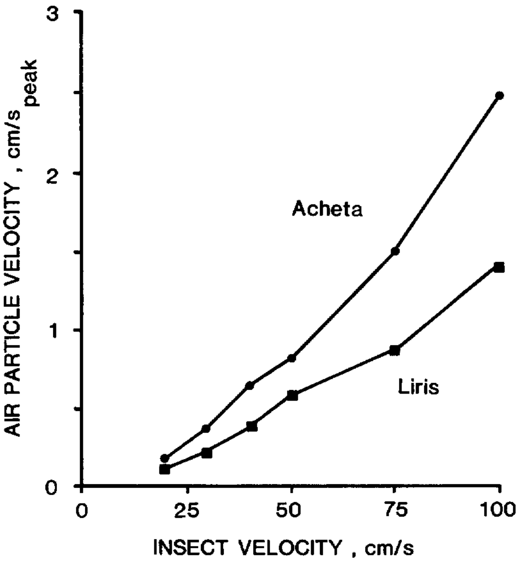

Fig. 2. Air particle velocity generated during artificial movement of bodies of *Acheta domesticus* (length: 25 mm) and *Liris niger* (length: 15 mm) along their long axis. The electret membrane of the microphone was positioned with its plane perpendicular to the animals' plane of movement. At a particular movement velocity the *Acheta* body generates stronger air particle movement than the *Liris* body. But considering the natural running speed of a cricket (< 10 cm/s) and a digger wasp (up to 50 cm/s) the running wasp generates much stronger air movement than a running cricket

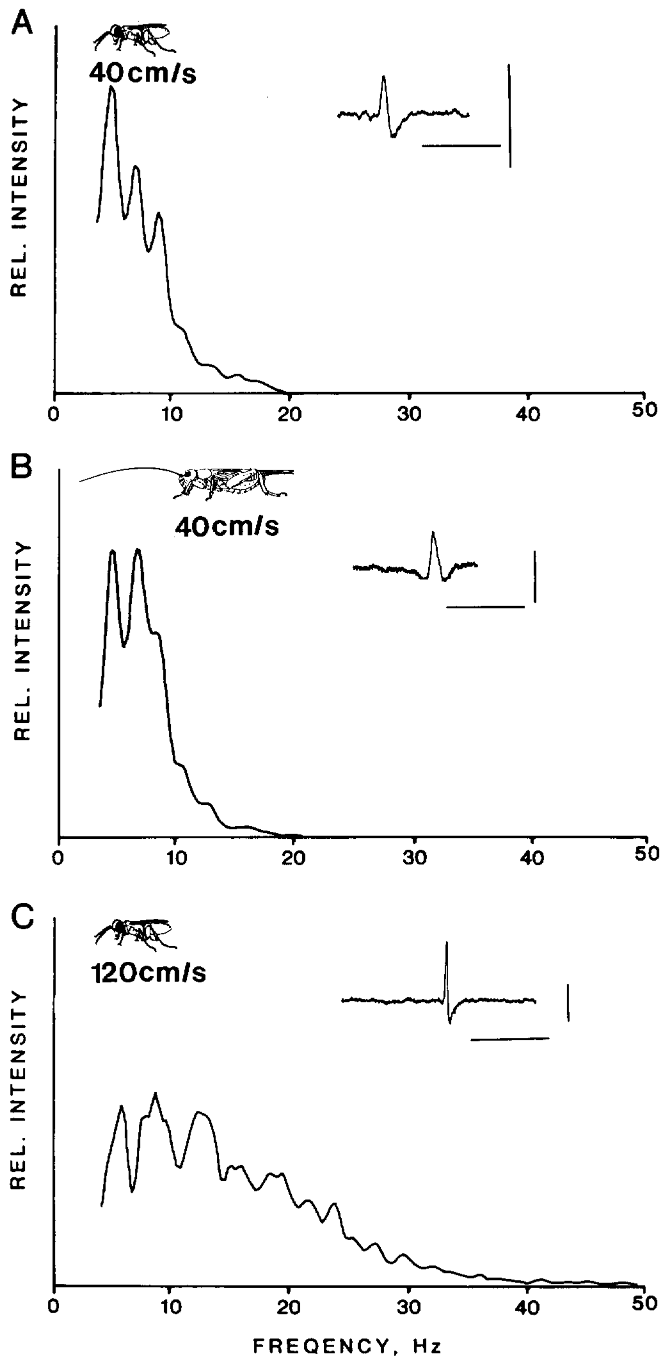

Fig. 3 A–C. Frequency spectra and microphone recordings (insets) from signals generated by bodies of *Acheta* and *Liris* which were moved with constant velocity along the microphone probe. **A** *Liris*, 40 cm/s; **B** *Acheta*, 40 cm/s; **C** *Liris*, 120 cm/s. Cal.: 500 ms, 100 mV. At all velocities tested (**A**, **B**) the main components of the spectra are below 20 Hz, relatively independent from the body shape and size (compare **A** and **B**); with increasing velocity the spectrum gets broader and includes higher frequencies (**C**)

Under laboratory conditions crickets running toward or passing each other usually do not elicit the 'headstand'-behavior. We tried to find differences of the signals produced by wasps and crickets, and moved bodies of *L. niger* and *A. domesticus* with different velocities (20–100 cm/s) along the microphone and measured the peak air particle velocities produced (Fig. 2; length of *L. niger* was 15 mm, of *A. domesticus* 25 mm excluding antennae; the body diameter of an *A. domesticus* is much larger than of *L. niger*). We used no velocities below 20 cm/s because the signals produced were too small to be recorded by the microphone. In order to extrapolate down to this range we determined the general slopes of the curves, including velocities higher than the natural ones (see below). At each given velocity the body of an *A. domesticus* generated stronger signals than the *L. niger* body. Measured air particle velocities ranged from 0.2 cm/s to 2.5 cm/s (Fig. 2) and depended strongly on the distance of the microphone probe from the animal's path (at these extreme near field conditions the attenuation of signal intensity with distance r can be approximated by $1/r^3$; for lit. see Tautz 1979). Frequency spectra of the signals of both insect bodies were very similar and contained energy mainly at frequencies below 20 Hz (determined for a movement velocity of 40 cm/s; Fig. 3A, B). The spectrum broadened with increasing movement velocity (Fig. 3C).

Running velocity of the two insect species during normal behavior differs greatly. Crickets rarely run faster than 10 cm/s (Schmitz et al. 1982; Thorson et al. 1982) while wasps in 'hunting mood' can reach speeds of 25–50 cm/s (Gnatzy and Heußlein 1986). Consequently the signal produced by hunting *L. niger* is more intense and contains energy at a broader frequency spectrum including higher frequency components than the spectrum elicited by a running cricket.

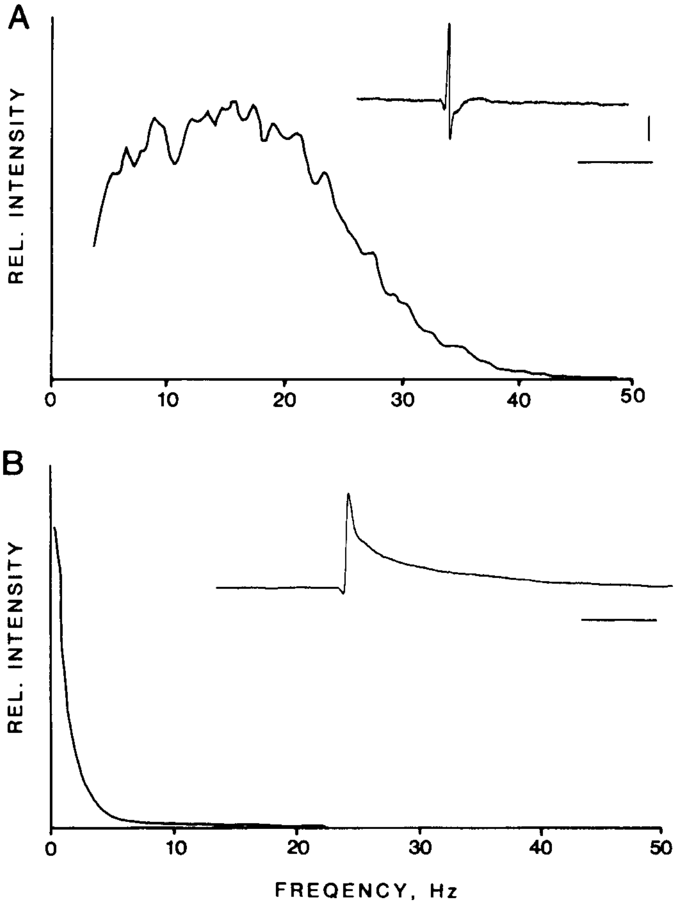

Fig. 4A, B. Signals generated by a simple styrofoam model. **A** frequency spectrum and microphone recording (inset) from a signal generated if the model passed the microphone with 120 cm/s. Spectrum and signal shape are very similar to the one obtained with a moving *Liris* body (Fig. 3C); only the amplitude of the signal produced by the model is higher, due to the larger size of the object compared to the size of the insect. This shows that the shape of the moved object has little influence upon the frequency composition of the signal produced. **B** frequency spectrum and signal (inset) recorded with a thermistor anemometer instead of the microphone. The signal shows strong long lasting air currents after the model passed the probe, corresponding to frequency components below 5 Hz. Cal.: 500 ms, 200 mV; anemometer uncalibrated

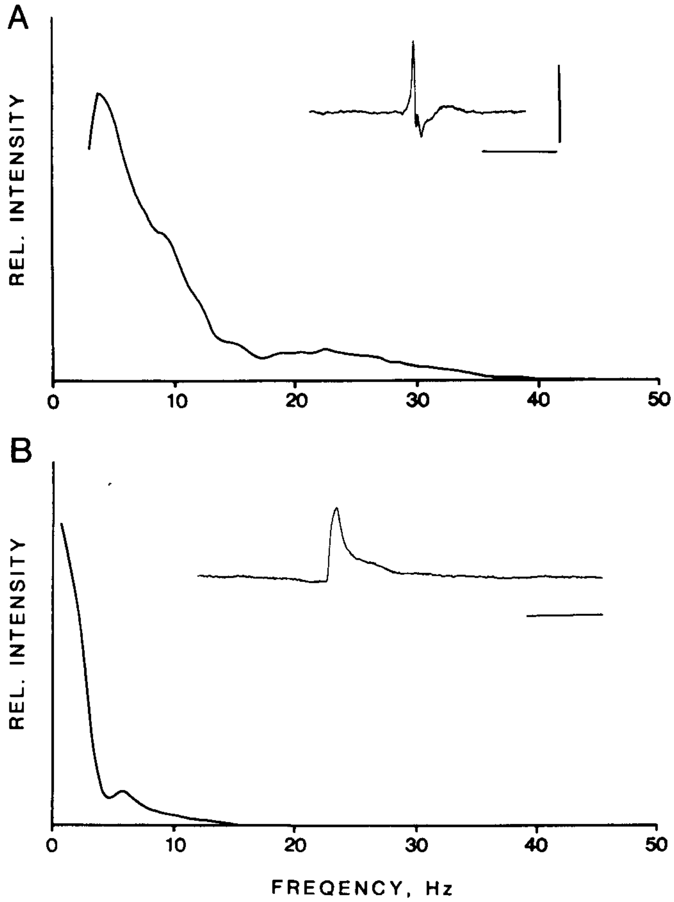

Fig. 5A, B. Signals generated by a styrofoam model that was stopped directly in front of the measuring probe. **A** microphone recording (inset) and frequency spectrum, **B** thermistor anemometer recording (inset) and frequency spectrum. The spectrum of the microphone recording (**A**) has less components above 15 Hz than the spectrum obtained if the specimen passed the microphone (Fig. 4A) and the signal amplitude is much lower. The anemometer recording (**B**) shows long lasting air currents after the model stopped and frequency components below 5 Hz, similar to the data shown in Fig. 4B. Cal.: 500 ms, 200 mV; anemometer uncalibrated

The shape of the moved body had very little effect on the frequency spectrum (Fig. 3A, B; recorded at a velocity of 40 cm/s). A test at a relatively high velocity of (120 cm/s) which results in broader spectra confirmed this: A simple styrofoam block with a shape very unlike a wasp and moved with the same velocity as a *L. niger* body, generated signals and spectra very similar to those produced by the wasp's body (Fig. 3C and Fig. 4A).

Using the styrofoam dummy, we also compared signals picked up by the microphone and the anemometer. Figure 4A, B shows the signals and frequency spectra obtained when moving the dummy along the probes at 120 cm/s. The microphone response (Fig. 4A) is very short and contains a broad frequency spectrum up to 50 Hz but no low frequencies while such frequency components can be demonstrated in the anemometer signal (Fig. 4B). Moreover, it can be seen that it takes several hundred milliseconds until the signal reaches the baseline after the dummy passes the probe; this means that there are long lasting air currents caused by the passing dummy.

Figure 5A, B shows the results for a situation in which the dummy was stopped from high velocity (120 cm/s) directly in front of the probes. Compared to the signals produced by the passing dummy (Fig. 4A, B), the frequency spectra contain fewer high frequencies. The frequency spectrum of the anemometer signal still shows a strong increase toward low frequencies, correlated to long lasting currents after the dummy stopped.

Discussion

Low frequency air particle movement has been described to play a role in intraspecific communication of crickets (Kämper and Dambach 1979, 1981) and in predator detection by caterpillars (Tautz 1977; Tautz and Markl 1978) and cockroaches (Camhi et al. 1978). The present study demonstrates that *Liris niger* produces air particle movements with a velocity up to 1–2 cm/s at frequencies below 20 Hz, measured close to the running course. Such signals can be detected by crickets with their cercal filiform hairs (Gnatzy and Heußlein 1986). Kanou and Shimozawa (1984) have reported thresholds of less than 0.03 mm/s for interneurons which receive input from these filiform hairs, and some of the interneurons exhibit even lowpass characteristic by responding only to stimulus frequencies below about 50 Hz (Kämper 1984); this range fits the frequency spectra measured in the present study.

With the same filiform hair/interneuron system by which the cricket detects a hunting *L. niger*, it also can hear the rhythmic, low frequency 30 Hz song components of a stridulating conspecific male (Kämper and Dambach 1985). However, the signals produced by *L. niger* are not rhythmic oscillations but single air puffs. It may be this difference used by the cricket to discriminate between the two possible sources and to trigger the appropriate reaction. It has been shown that some of the interneurons reflect the frequency of rhythmic air particle oscillations near the cerci by phase-locked spiking (Kanou and Shimozawa 1984; Kämper 1984); this information is transmitted by ascending axons to the thoracic ganglia (Mendenhall and Murphey 1974) and to the head ganglia (Kämper, unpublished data). Where and how the recognition process takes place and where and how the correct behavioral response is triggered is presently unknown.

Filiform hairs are very sensitive receptors for air particle movements. Compared with their sensitivity and working range (<0.03 mm/s, <1 Hz–1 kHz) the technical probes used in the present study have a limited performance. Additionally the electret membrane of the microphone is too large (about 6 mm in diameter) to detect local air currents. The anemometer probe on the other hand is very small (<1 mm), but has no directional sensitivity; in addition, it reaches its maximum sensitivity only after the hot air surrounding the thermistor has moved away; therefore, a single air puff can not be correctly recorded (especially the higher frequency components). Hence we cannot exclude that more components than demonstrated here occur within the signal produced by *L. niger*. This applies especially to very low intensity oscillations that might be caused by the leg movements of the wasp.

This study has shown that the velocity of the running wasp affects the spectral composition of airborne signals produced during approach towards the prey. This does not necessarily mean that it is the air particle velocity which is the effective parameter involved in triggering the 'head-stand' behavior of crickets. In the cockroach, air particle acceleration is the effective signal parameter for escape (Plummer and Camhi 1981). For the filiform hairs of crickets there is evidence that they discriminate between air particle velocity and acceleration, using different populations of cercal filiform hairs (Shimozawa and Kanou 1984).

In a pilot experiment we tried whether 'head-stand' behavior of crickets can be elicited by signals generated by an artificially moved *Liris* body. Only in rare cases crickets showed a weak response by lifting the abdomen; so we conclude that this pure air puff signal does not yet contain all components necessary to trigger the head-stand behavior. Those components missing could be, e.g., very low intensity air-borne vibrations (see above). From previous experiments (Gnatzy and Heußlein 1986) we can exclude visual stimuli or substrate vibrations being involved in releasing the 'head-stand' behavior.

Liris niger is specialized for hunting exclusively crickets (Gnatzy et al. 1989). The wasps face two problems: (a) to locate a cricket; according to own observations the number of crickets in the wasp's biotop is limited; (b) to overcome the cricket's highly efficient predator detecting system, i.e., the cercal filiform hairs. Hunting by flight and optical identification of prey would increase the chance to find crickets; but flying insects produce air particle oscillations in the rhythm of their wing beats which can be detected by the filiform hairs. Crickets detect the strong air currents modulated at 120 Hz which are produced by flying *L. niger* over distances of about 15–20 cm (Gnatzy and Heußlein 1986). They react to the airborne sound with cessation of movement.

The strategy of *L. niger* to overcome an early recognition by the crickets is to run very fast on the ground and so literally avoid the cricket's flying predator detecting system. Crickets are able to recognize running wasps only within a radius of about 1–3 cm from their cerci; thus, considering the speed of the wasp, a cricket has a reaction time of only about 100 ms available between the detection of the predator and an escape or adequate defence behavior (Gnatzy and Heußlein 1986), before it is touched by the wasp and recognized as prey.

Another hunting strategy for the wasp would be to run at slower speed in order to reduce the intensity of the treacherous airborne signals (Fig. 2) and thus to come even closer to the crickets. But this could result in a reduced chance to find the prey, because only a limited area could be explored within the few hours of the day which are suited for hunting.

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