

## ULTRASOUND AVOIDANCE BEHAVIOUR IN THE BUSHCRICKET *TETTIGONIA VIRIDISSIMA* (ORTHOPTERA: TETTIGONIIDAE)

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### Summary

The responses of female *Tettigonia viridissima* to simulated bat echolocation calls were examined during tethered flight. The insects responded with three distinct behaviours, which occurred at graded stimulus intensities. At low intensities (threshold 54 dB SPL), *T. viridissima* responded by steering away from the sound source (negative phonotaxis). At intensities approximately 10 dB higher, beating of the hindwing was interrupted, although the insect remained in the flight posture. A diving response (cessation of the wingbeat, closure of the forewings and alignment of the legs against the body) occurred with a threshold of 76 dB SPL. Considering these thresholds, we estimate that the diving response occurs at approximately the sound amplitude at which many aerial-hawking bats first receive echoes from the insect. The other behaviours

probably occur before the bat detects the insect and should therefore be interpreted as early avoidance behaviours.

The repertoire of startle responses in *T. viridissima*, with directional and non-directional components, is similar to those of crickets and moths, but quite different from those described for another bushcricket (*Neoconocephalus ensiger*), which shows only a non-directional response. This supports the conclusion that bat-evasive behaviours are not conserved within the Tettigoniidae, but instead are shaped by the ecological constraints of the insects.

Key words: bat/insect interaction, predator avoidance, hearing, negative phonotaxis, startle behaviour, bushcricket, *Tettigonia viridissima*.

### Introduction

Several groups of nocturnally flying insects are known to evade the attacks of insectivorous bats by monitoring the echolocation calls of hunting bats (e.g. Roeder, 1967; Miller and Olesen, 1979; for reviews, see Hoy, 1992; Hoy, 1994). While in most of these groups hearing probably evolved primarily for this purpose (e.g. Lepidoptera, Neuroptera, Coleoptera; for a review, see Hoy, 1992), in ensiferans (Tettigoniidae and Gryllidae), bat avoidance seems to be a secondary function of the hearing system: intraspecific acoustic communication probably evolved long before the appearance of bats (Alexander, 1962; Gwynne, 1995). Because of the two contexts of hearing, there is a need to discriminate between the signals of conspecific communication partners and of predators to avoid interference between the recognition of conspecifics and the detection of predators.

Bat-avoidance behaviours during flight have been described in several species of cricket (Hoy et al., 1989). These behaviours include directional (negative phonotaxis) and non-directional (Popov and Shuvalov, 1977) components and are similar to those described for several groups of moth (for a review, see Surlykke, 1988). Because the communication signals of crickets are mostly limited to low frequencies (below 12–15 kHz), discrimination between bats and conspecifics is

based mainly on the spectral properties of the signal, with positive phonotaxis elicited by low frequencies and bat-avoidance reactions elicited by ultrasonic signals (Popov and Shuvalov, 1977; Moiseff et al., 1978).

In most tettigoniids (bushcrickets), communication signals extend well into the frequency range between 20 and 60 kHz (Heller, 1988), the range used by most aerial hawking bats (Fenton et al., 1998). Although bushcrickets are easily able to hear and localize ultrasound (e.g. Kalmring et al., 1990) and many species are nocturnal, reports of bat avoidance are rare for this group. Libersat and Hoy (Libersat and Hoy, 1991) describe a startle response for flying *Neoconocephalus ensiger* (subfamily Copiphorinae), which dive in response to ultrasound, but fail to show any directional response with respect to the sound source. Calling, non-flying males of the same species interrupt calling when stimulated with ultrasound (Faure and Hoy, 2000). The thresholds for startle behaviour during calling and flying were similar at approximately 75 dB SPL, which is 30–40 dB above the hearing threshold.

Field measurements of the hearing range of bushcrickets for bats suggest that the insects hear the echolocation calls of bats long before the bat can detect the returning echo (Schul et al., 2000). The absence of directional responses to bat calls in *N.*

*ensiger* seems surprising, since their sensory abilities would allow bushcrickets to perform negative phonotaxis to avoid being detected by the bat. It remains uncertain whether *N. ensiger* represents the general pattern of bat avoidance in bushcrickets or whether other groups of tettigoniids show more complex behaviours in response to bat calls.

In the present work, we tested the responses of female *Tettigonia viridissima* to synthetic bat calls during tethered flight. The phonotactic behaviour of this long-winged bushcricket has been studied in detail. The male song of this species covers a frequency range from 10 to 60 kHz (Heller, 1988), and females use mainly the ultrasonic components for localization (Jatho, 1995). For song recognition during phonotaxis, females evaluate a variety of temporal cues (Schul et al., 1998; Schul, 1998), and the neuronal processing of the spectral and temporal song characteristics at the thoracic level has been described in detail (Schul, 1997). Because acoustic communication normally takes place at night (Schul, 1994) and females often perform phonotaxis during flight (W. Schulze and J. Schul, personal observations), this species seems to be vulnerable to predation by aerial hawking bats. This species, like other tettigoniids, was found to be part of the diet of bats (Arlettaz, 1995). We describe a variety of evasive behaviours that occur in response to bat calls at graded intensity levels during simulated approaches of bats towards the bushcricket.

### Materials and methods

Female *Tettigonia viridissima* L. were collected as adults and nymphs from wild populations near Erlangen, Germany. The females were kept in the laboratory under an artificial photoperiod of 14h:10h L:D. Experiments took place in a sound-proofed room (2 m×2 m×3 m) lined with 10 cm foam wedges. The ambient temperature was 22–25 °C, and the room was illuminated only by the red light of the position detector (see below). The insects were tethered at the pronotum and placed ventral side up 20 cm in front of a fan producing a windstream. The airstream was laminarized by straws (length 5 cm) placed in front of the fan. In this situation, the females adopted the flight posture and started beating their wings. The flight posture involves holding the front legs straight out in front of the head and the mid- and hindlegs straight back against the abdomen (see Fig. 2A). The forewings were fully opened perpendicular to the animal's longitudinal axis. In *T. viridissima*, the wingbeat is performed mainly with the hindwings, accompanied by relatively small movements of the forewings, as has also been described in crickets (May et al., 1988). During tethered flight, females of *T. viridissima* showed steering responses, moving their abdomen towards songs of conspecific males. The activity of the insect was observed by a video camera placed above the tethered bushcricket.

Movements of the abdomen were monitored with an optoelectronic position detector (von Helversen and Elsner, 1977). A piece of reflective foil (2 mm×2 mm, Scotchlite) was attached to the base of the ovipositor, and the hindwings were shortened so that they did not cover the reflective foil. The

position detector converted movements of this reflective foil perpendicular to the insect's long axis into an electrical signal, which was displayed on an oscillograph and recorded on an eight-channel DAT recorder (Sony PC 208A) for later analysis. The position detector monitored not only steering responses, but also movements of the ovipositor due to wingbeats, abdominal ventilation and other body movements. To classify a signal from the position detector as a steering response, we always checked the corresponding video recording visually.

Electromyograms (EMGs) of the flight muscles of the hindwings were recorded to monitor the flight activity of the bushcricket. Two copper wires (diameter 55 µm), insulated except at the tip, were inserted through small holes in the pro- and metathoracic pleurites. The recorded signals were amplified using a custom-designed amplifier, bandpass-filtered (100–3000 Hz) and stored on a separate track of the DAT recorder.

### Acoustic stimulation

The stimuli were delivered *via* two loudspeakers (Technics EAS10TH400C) located 50 cm from the preparation, at 60° (frontal) to the body axis on both sides of the animal. The signals were generated using a computer-based D/A converter system with 12-bit resolution and a sampling rate of 350 kHz. The signals were amplified and their amplitude attenuated under the control of the computer. The amplitude of the signals was calibrated with a condenser microphone (Bruel & Kjaer 4135 or 4138) and a Bruel & Kjaer (2209) sound level meter using its 'peak hold' function. All signal amplitudes are given in dB peak SPL re  $2 \times 10^{-5}$  Pa. Sound measurements were obtained at the position of the animal, but with no animal present.

We used a synthetic bat echolocation call of the frequency-modulated (FM) type. The call was 8 ms in duration and frequency and was modulated from 65 to 28 kHz, with the main energy concentrated at approximately 30 kHz. Such calls are typical of larger vespertilionid bats (e.g. *Myotis myotis* and *Eptesicus serotinus*) during searching flight in free air space (Weid and von Helversen, 1987).

Two experimental series were used. The first simulated an echolocating bat flying towards the insect, assuming a call amplitude of 110 dB SPL at 25 cm distance, a flight speed of 5.5–6 m s<sup>-1</sup>, spreading loss of 6 dB per double distance and atmospheric attenuation of 1 dB m<sup>-1</sup> (Lawrence and Simmons, 1982; Sivian, 1947). Each simulated bat approach consisted of 26 calls with a call period of 173 ms and with amplitudes increasing from 44 dB (approximately 25 m distance from the bat) to 94 dB SPL (approximately 1 m from the bat). Four repetitions of the simulated approach were tested for each side of each insect.

The second experimental series was used for a quantitative analysis of the behaviours observed in the first experiment. Stimuli consisted of seven synthetic bat calls of constant amplitude and with a call period of 173 ms. Each intensity was tested four times from both sides of the insect. Experiments started at 43 dB SPL, and intensities were normally increased

in steps of 3 dB up to 91 dB SPL. The behavioural threshold criterion was two successive responses out of the four repetitions tested on each side. Latencies were measured as the time between the sound reaching the insect and the onset of the response (steering) or the time when the first action potential related to the wingbeat was missing in the EMG recordings. The two hemispheres of each insect were treated independently.

After being placed in the airstream, female *T. viridissima* normally started to fly immediately, and they flew continuously after approximately 1 min. We first tested the simulated bat approaches, then used the series with seven bat calls for threshold determination. Because preliminary experiments showed a strong tendency of the insects to adapt to repeated stimuli, a silent period of at least 4 min (approach series) or 2 min (threshold series) was inserted between the stimulus repetitions. Nevertheless, some long-term adaptational effects could be observed towards the end of each experiment. Because *T. viridissima* do not fly indefinitely when tethered, the duration of the silent intervals was a compromise that allowed us to test the complete stimulus set for most individuals while accepting only minor adaptation effects.

## Results

In the first set of experiments, we stimulated flying *T. viridissima* females with simulated bat approaches. In these experiments, we wanted to reveal the bat-evasive behaviours and describe them in their functional context. All the insects ( $N=11$ ) responded with a variety of behaviours to this series of echolocation calls of increasing intensity (Fig. 1). With low call amplitudes, the insects continued their normal flight with a wingbeat rate of approximately 15–16 Hz. This rate can be seen in the EMG recording (Fig. 1B) and also in the position detector recording of abdominal movements (Fig. 1A, before arrowhead 1). When the bat calls reached an amplitude of 55–60 dB SPL, the insects showed a steering response away

from the loudspeaker. This steering response includes bending the abdomen away from the speaker and flexing the legs in the same direction (Fig. 2B). The abdominal steering response can also be detected in the signal from the position detector (Fig. 1A, arrowhead 1).

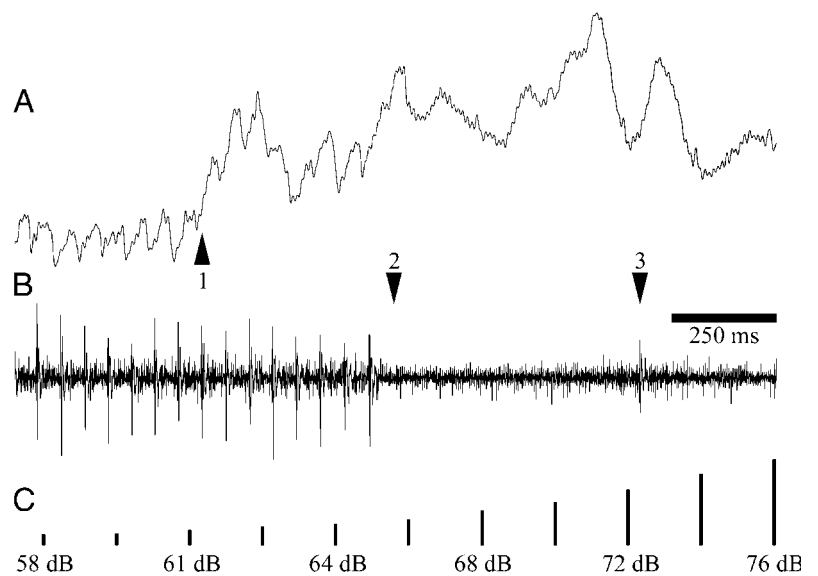
With increasing intensities of the bat calls, the bushcrickets stopped beating their hindwings, but remained in the normal flight posture with the forewings fully opened perpendicular to the animal's longitudinal axis and with the forelegs held out in front of the head. During this behaviour, rhythmic activity in the EMG recordings ceased (Fig. 1B, arrowhead 2). At the same time, the correlated oscillation in the position detector signal disappeared. Because the second experimental series (see below) demonstrated that the insects resumed beating their wings shortly (0.3–1 s) after the bat calls stopped, we refer to this behaviour as 'wingbeat interruption'.

When the intensity of the bat signal increased still further, the forewings of the insect were folded abruptly backwards into the resting position, and the front legs were moved backwards and held along the thorax. In the EMG, a spike often appeared concomitantly with the folding of the forewings (Fig. 1B, arrowhead 3). Since we suspect that this rapid behaviour leads to sudden descent (see Discussion), we refer to it as 'diving'. Following the end of each stimulation series, the insects resumed normal flight either spontaneously or after external stimulation, e.g. a flash of light or an air puff onto their ventral side.

The experiments with the simulated bat approach revealed three distinct responses of *T. viridissima*, elicited at graded intensity levels: steering, wingbeat interruption and diving. The second set of experiments, with each stimulus consisting of seven echolocation calls of equal amplitude, was used to perform further quantitative analysis of these behaviours.

We found the same set of behaviours in the second experimental series. At lower stimulus intensities, *T. viridissima* showed steering responses away from the sound source (Fig. 3A). At higher intensities, the insects interrupted

Fig. 1. Response of a female *Tettigonia viridissima* during tethered flight to a simulated bat approach. (A) Position detector recording of abdominal movements. (B) Electromyographic (EMG) recording of the flight muscles. (C) Timing of the synthetic echolocation calls, with sound pressure levels indicated for every other call (amplitudes are not drawn to scale). The stimulus direction was from below relative to the abdominal position trace. The insect initiates a steering movement away from the loudspeaker (arrowhead 1). The hindwing beats are visible as EMG spikes and also as oscillations in the position trace. Wing beating stops approximately 400 ms after the steering response (arrowhead 2 indicates the first missing EMG spike). After the wingbeats stop, strong abdominal pumping is visible in the position trace (A). The single spike in the EMG (arrowhead 3) marks the folding of the forewings.



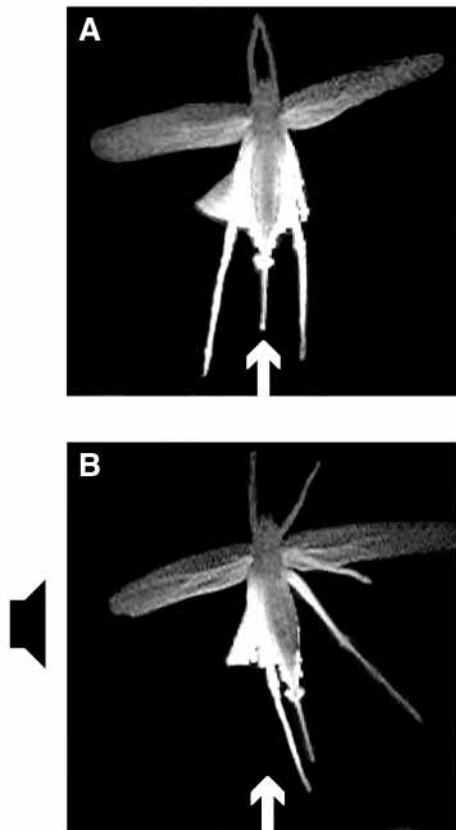


Fig. 2. Steering response of a tethered flying *Tettigonia viridissima* in response to a simulated bat approach. (A) Tethered flight without stimulation. (B) The steering response after an echolocation call at 77 dB SPL. The direction from the loudspeaker to the animal is indicated. The white arrows in A and B indicate the position of the ovipositor during undisturbed tethered flight.

the beating of the hindwings, while remaining in the flight posture (Fig. 3B,C). The interval after which the wingbeat resumed was variable: in some cases, it started before the end of the stimulus (Fig. 3B), whereas in others the interruptions lasted for several seconds (Fig. 3C). During stimulation that elicited wingbeat interruption, the insect often did not show steering responses (Fig. 3C). At still higher echolocation call intensities, the insects responded with diving, i.e. they stopped beating their wings, folded the forewings and took their legs out of the flight posture. All the insects tested ( $N=10$ ) showed the first two behaviours (steering and wingbeat interruption), but we did not reach the threshold criterion for diving with all insects within the intensity range tested (43–91 dB SPL): two did not show this behaviour at all, another two only during stimulation from one side, but not from the other.

The thresholds for these three behavioural responses are given in Fig. 4. Steering responses occurred at call amplitudes of 53.5 dB SPL (median), while wingbeat interruption took place at intensities approximately 10 dB higher (64 dB SPL). The diving response occurred after an additional increase in amplitude of 12 dB (76 dB SPL).

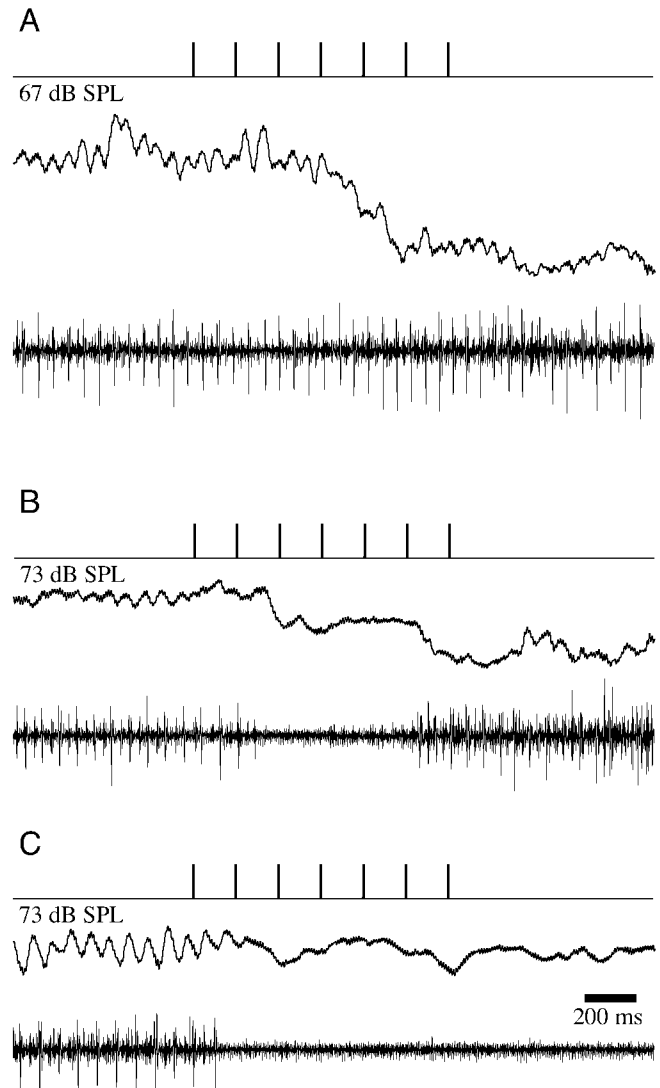


Fig. 3. Responses of tethered flying *Tettigonia viridissima* to a series of seven synthetic bat calls. The timing of the stimuli is indicated in the top trace of each figure; the stimulus intensities are given. The middle traces are position detector recordings of abdominal movements; the bottom traces are electromyographic (EMG) recordings. (A) The insect responds with a steering response away from the sound source. (B) The insect stops beating its wings, but starts again before the stimulus is over. (C) The insect stops beating its wings. Note the differences in the EMG recordings before and after the stimulation in A and B.

The flight pattern after an episode of steering or wingbeat interruption differed from that before the response. This was observed in changes in the EMG pattern (Fig. 3B) and in a small but significant change in wingstroke rate, which increased from  $15.8 \pm 2.7$  Hz before to  $16.5 \pm 3.2$  Hz after stimulation (means  $\pm$  s.d.,  $N=7$  with five trials per insect, 25–30 wingbeat cycles both before and after stimulation;  $P < 0.05$  paired  $t$ -test).

At lower stimulus intensities, responses often occurred only after several echolocation calls had reached the insect

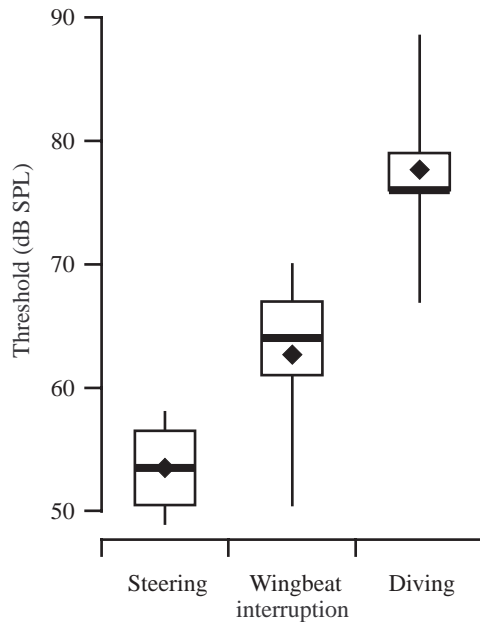


Fig. 4. Box-and-whisker plots of the thresholds for three behaviours of tethered flying *Tettigonia viridissima* in response to a series of simulated bat calls. The box indicates the 25th and 75th percentiles, and the whiskers indicate the 10th and 90th percentiles. Bold lines give the median, and the diamonds give the mean. In the diving response, more than 25% of the females had thresholds at the median value (steering and interruption of wingbeat,  $N=20$  in 10 insects; diving,  $N=14$  in eight insects).

(Fig. 3A,B), although in other cases one call was sufficient to elicit a response (Fig. 3C). To measure the behavioural latencies, we used only responses to the first call of the stimulus. For stimulus amplitudes above 75 dB, the behavioural latencies were  $74 \pm 20$  ms (mean  $\pm$  s.d.,  $N=5$  with 3–20 trials per insect). In addition to these behavioural latencies, some EMG recordings revealed action potentials with latencies of  $29 \pm 6$  ms (mean  $\pm$  s.d.,  $N=5$ , 1–15 trials per insect) in response to the first call of a stimulus (Fig. 5). Although we did not identify the origin of these action potentials, they appeared to be correlated with movements of the hindlegs.

### Discussion

This study shows that the bushcricket *T. viridissima* responds with several distinct behaviours to ultrasonic stimulation that mimics the echolocation calls of bats. These behaviours are graded according to the stimulus intensity and have several characteristics in common with the ultrasound-induced behaviours of other flying insects (for a review, see Hoy, 1992). Nevertheless, these behaviours are quite different from the acoustic startle described for another bushcricket, *Neoconocephalus ensiger*, which shows only a non-directional type of response to ultrasound stimulation: the insect interrupts the wingbeat, folds all four wings backwards and takes the forelegs out of the normal flight posture (Libersat and Hoy,

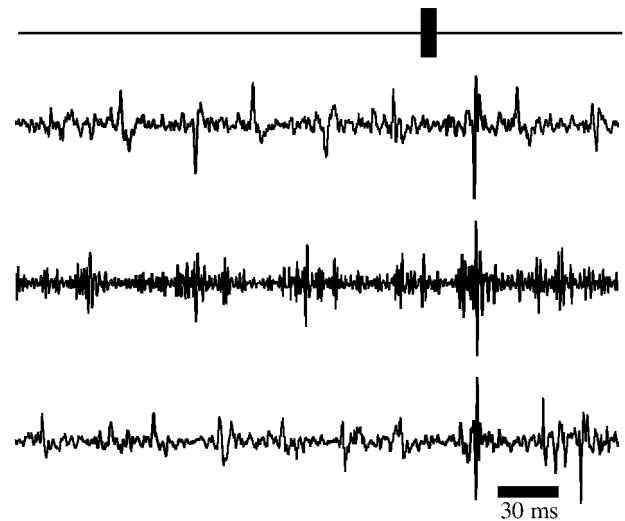


Fig. 5. Electromyographic (EMG) recordings from tethered flying *Tettigonia viridissima* during stimulation with synthetic bat calls. The timing of the first call (out of a series of seven) is given above the top trace. In some preparations, fast responses occurred in the EMG recording at latencies shorter than 30 ms, while rhythmic activity correlated with the wingbeat continued. Stimulus amplitude 81–84 dB SPL; the recordings are from three different preparations.

1991). A directional steering response, as we describe here for *T. viridissima*, was not present, and the non-directional response of *N. ensiger* also differed from the non-directional components of the behaviour of *T. viridissima*: in *T. viridissima* during ‘wingbeat interruption’, the legs and forewings remained in the flight posture, but in *N. ensiger* the forelegs and all four wings were aligned along the body. In addition, when *T. viridissima* left the flight posture and closed their forewings (‘dive’), they did not resume beating their wings for several seconds, while in *N. ensiger* the interruption of the wingbeat lasted for only a few hundred milliseconds (Libersat and Hoy, 1991). Although the *Tettigonia* are closely related to *Neoconocephalus* (Gwynne, 1995), the ultrasound avoidance behaviour of the former resembles that of the more distantly related crickets, in that it contains both directional and non-directional components (Hoy, 1992). This suggests that bat-avoidance strategies are not conserved within this phylogenetic group, but instead shaped by the ecological requirements of each species. Differences in the bat communities and in the ecology of the insect are likely to affect predation pressure, requiring different countermeasures by the insects. Considerable differences in responsiveness to bat calls appear within the Mantodea (praying mantis, Yager et al., 1990; Hoy, 1992), and the presence or absence of bats has been shown to influence the hearing system in moths (Fullard, 1994; Surlykke, 1988). Attempts to understand the interactions between bat avoidance and the communication system of one bushcricket species should therefore avoid extrapolating from the avoidance behaviour of other species.

At low echolocation call intensities (mean 53.5 dB SPL), flying *T. viridissima* show a steering response away from the

source of the echolocation calls, including fast abdominal ruddering and extension of the contralateral mid- and hindleg. Leg extension impairs the path of the contralateral hindwing, reducing the thrust on this side of the insect (May and Hoy, 1990). Together with the rapid change in the centre of gravity due to abdominal movements, this should lead to a turn in the flight path. The flexing of the body probably also influences the tilt of the front- and hindwings, further increasing this turning tendency, as has been found in crickets (May et al., 1988). In response to echolocation calls of higher intensities, *T. viridissima* interrupt the beating of their hindwing, but remain in the flight posture, i.e. the forewings remain in their extended position. This would lead in free flight to a loss of height and, depending on the duration of the interruption, the insect would either continue normal flight or land on the ground. At still higher intensities, the bushcrickets rapidly close their forewings and leave the flight posture completely, probably entering a sudden dive, inevitably resulting in landing on the ground or on vegetation.

To determine the relevance of these behaviours in the field, we must consider the detection distances of aerial hawking bats for insects. Several studies have measured the detection distances of bats for small insects (e.g. Kalko and Schnitzler, 1989; Kalko and Schnitzler, 1993; Miller and Olesen, 1979), but few data are available regarding larger insects such as *T. viridissima*. In training experiments, the big brown bat *Eptesicus fuscus* was able to detect spheres 19 mm in diameter (which cause echoes of similar amplitude to those from medium to large insects) at distances of up to 5 m (Kick, 1982).

Using the thresholds given in Fig. 4, we can estimate the distances between the echolocating bat and the insect at which the different behaviours occur. Assuming an echolocation call amplitude of 110 dB SPL at 25 cm in front of the bat (Jensen and Miller, 1999; Griffin, 1958) and an atmospheric attenuation of 1 dB m<sup>-1</sup> (Lawrence and Simmons, 1982), the median thresholds for steering (54 dB SPL) and interruption of the wingbeat (64 dB SPL) would correspond to distances of approximately 18 m and 10 m, respectively. Therefore, both behaviours can be classified as early-warning behaviours, because they occur before the bat detects an echo from the insect. Both behaviours probably function to move the insect away from the search cone of the bat, the area to which effective echolocation is limited because of the directionalities of call radiation and hearing (e.g. Hartley and Suthers, 1989). Stopping the movements of the hindwings and aligning them along the abdomen also reduces the reflecting surface of the insect and the probability of glints, high-amplitude echoes caused by wing positions perpendicular to the direction of the incident sound (Kober and Schnitzler, 1990). Thus, the interruption of hindwing beating also reduces the amplitude of a potential echo, further lowering the probability of being detected by the bat.

The threshold for diving behaviour (leaving the flight posture, closure of the forewings) of 76 dB SPL corresponds to a bat-to-insect distance of approximately 5 m, which is roughly

the distance at which the bat should be able to detect an echo from the bushcricket. This behaviour is therefore comparable with the dives of lacewings *Chrysopa carnea* (Miller and Olesen, 1979), which also occur at approximately the detection distance of the bats. From the moment when the diving behaviour in *T. viridissima* occurs, a bat would need at least 1 s to reach the insect (Kalko and Schnitzler, 1989). This latency between the dive and the arrival of the bat is too long for the dive to be classified as a 'last-chance' reaction. Such 'last-chance' manoeuvres were described for lacewings and moths that respond with erratic changes in their flight (or falling) path immediately before the bat reaches them, without leaving enough time for the bat to correct its course (Miller and Olesen, 1979; Roeder, 1967). Whether a last-chance response exists in *T. viridissima* was not tested in this study, because it should occur at higher echolocation call intensities than those used here.

#### *Comparisons with behavioural thresholds of other insects*

One problem in comparing the behavioural thresholds for bat evasion of the different insect groups arises from the various types of stimuli used in the different studies. Here, we used artificial echolocation calls (duration 8 ms) with the characteristic frequency modulation of the calls of most insectivorous bats (Fenton et al., 1998), while other studies used pure tones of varying duration (e.g. Libersat and Hoy, 1991) or pulse trains with varying pulse duration and rate with constant carrier frequencies (e.g. Yager et al., 1990). Because of the integration time of the receptor cells (Surlykke et al., 1988), both the duration of the stimulus and the type of stimulus (frequency-modulated or pure-tone) influence hearing sensitivity. In the bushcricket *Phaneroptera falcata*, the hearing threshold for a frequency sweep was more than 10 dB higher than for the corresponding pure tone (Schul et al., 2000). The threshold values obtained in the different studies are therefore difficult to compare.

A comparison of the behaviour of the green lacewings (*Chrysopa carnea*) and *T. viridissima* suggests that, in addition to these methodological problems, a comparison of absolute thresholds might not be relevant. In both cases, the 'diving responses' occur at approximately the distance (and hence the call amplitude) at which the bat should first detect an echo, 5 m (76 dB SPL) in *T. viridissima* and 0.5–2 m in the much smaller *C. carnea* (Miller and Olesen, 1979). The same functional behaviour, a dive just before the bat receives an echo, should therefore occur at quite different echolocation call amplitudes depending on the strength of the echo reflected by the insect. More relevant than comparing absolute echolocation call intensities, therefore, is a comparison of functional intensities, i.e. taking into consideration the echo detection range of the bats for various insects. This example also supports the idea that large insects require much better sensory abilities to protect themselves from bats because they cause larger echoes that can be detected at greater distances by the bat (Forest et al., 1995; Surlykke et al., 1999).

*Response latency – neuronal processing*

The latencies of acoustic startle behaviours in insects are generally short, with latencies below 100 ms reported in most groups (for a review, see Faure and Hoy, 2000). Although the latencies for *T. viridissima* (74±20 ms) are longer than the latencies reported for *Neoconocephalus ensiger* (45 ms during flight; Libersat and Hoy, 1991; 35 ms during calling; Faure and Hoy, 2000), we detected EMG responses (i.e. without the ‘mechanical latency’ until a movement is detectable) at latencies of only 29±6 ms. Such short times allow some speculation about the neuronal elements involved and the neuronal centres where the processing of ultrasound signals takes place. It has been suggested that a first-order auditory interneuron (T-fibre, TN-1) is involved in startle and evasive behaviours in bushcrickets (McKay, 1969; Libersat and Hoy, 1991). The characteristic anatomical features of this neuron are two axon collaterals, one connecting the dendritic regions in the prothoracic ganglion with the brain, and the other descending to the meso- and metathoracic ganglia. This morphology, together with the short behavioural latencies, led to the idea that startle responses in bushcrickets could be mediated from the prothoracic ganglion directly to the flight pattern generators in the meso- and metathoracic ganglia without involving the brain. Regardless of whether the startle response is mediated directly or through a loop *via* the brain, the short latency of 29 ms strongly suggests that neurons with a large axonal diameter and a high conduction velocity should be involved. Since TN-1 is the only auditory neuron fulfilling this requirement (Schul, 1997), it is a good candidate for this task.

Nevertheless, the high variability and especially the very strong habituation of the bat-evasive behaviours in *T. viridissima* suggest that TN-1 does not possess the command-neuron-like function of Int-1 (AN-2) in crickets (Nolen and Hoy, 1984): if we left a pause of only 1 min between stimulus repetitions, the insects ceased to respond within two or three presentations. In contrast, TN-1 does not habituate with stimulus repetitions every 10 s. We suggest that TN-1 is responsible for the fast latencies by triggering the responses, while habituation takes place in the brain circuitry that controls and modulates the bat-evasive behaviour. Such a division of labour between TN-1 and brain networks was also suggested for the control of male response calls in duetting bushcrickets, which occur with latencies as short as 25 ms (Robinson et al., 1986).

*Interference between bat detection and song recognition*

Song recognition in *T. viridissima* is based on several temporal characteristics, one of which is the duration of the pause between the double pulses. On a walking compensator, females responded only when this pause had a certain minimum duration, below which female responses dropped sharply (Jatho, 1995; Schul, 1998). There is evidence that interneuron TN-1, which is thought to serve a bat-detector function during flight (see above), is involved in filtering this variable during walking phonotaxis (Schul, 1997). A similar double function has been ascribed to an auditory interneuron

in crickets (Int-1=AN2), which controls bat evasion during flight (Nolen and Hoy, 1984) and is involved in song localization during walking (Schildberger and Hörner, 1988). If such a context-dependent gating of TN-1 occurs in *T. viridissima*, we should expect differences in selectivity of phonotaxis during flight and walking.

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