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## Sensory ecology of predator–prey interactions: responses of the AN2 interneuron in the field cricket, *Teleogryllus oceanicus* to the echolocation calls of sympatric bats

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**Abstract** We observed the responses of the AN2 interneuron in the Pacific field cricket, *Teleogryllus oceanicus*, a cell implicated in eliciting avoidance flight away from bats, to acoustic stimuli representing the echolocation calls of bats as well as field recordings of search and gleaning attack calls of six species of insectivorous sympatric bats (West Australia, Australia: *Tadarida australis*, *Chalinolobus goudii*, *Nyctophilus geoffroyi*; Queensland, Australia: *Vespadelus pumilus*, *Myotis adversus*; Kaua'i, Hawai'i: *Lasiurus cinereus*). The broad frequency sensitivity of the AN2 cell indicates that *T. oceanicus* has evolved to detect a wide range of echolocation call frequencies. The reduced sensitivity of this cell at frequencies higher than 70 kHz suggests that some bats (e.g., the gleaning species, *N. geoffroyi*) may circumvent this insect's auditory defences by using frequency-mismatched (allotonic) calls. The calls of the freetail bat, *T. australis* evoked the strongest response in the AN2 cell but, ironically, this may allow this bat to prey upon *T. oceanicus* as previous studies report that under certain conditions, flying crickets exhibit ambiguous directional responses towards frequencies similar to those emitted by this bat. Short duration calls (1–2 ms) are sufficient to evoke AN2 responses with instantaneous spike periods capable of causing defensive flight behaviours; most bats tested emit calls of durations greater than this. The short calls of *N. geoffroyi* produced during gleaning attacks may reduce this species' acoustic conspicuousness to this cricket.

**Keywords** Cricket · Bat · Echolocation · Auditory ecology

**Abbreviations** AN2: Ascending neuron 2 · dB peSPL: Decibel, peak equivalent sound pressure level · source level dB: Decibel intensity measured at 10 cm · IP: Instantaneous period · kHz: Kilohertz

### Introduction

The Pacific field cricket, *Teleogryllus oceanicus*, has been a valuable species for the examination of the neural processes integrating hearing and behaviour (Pollack and Hoy 1989; Pollack 1998). In laboratory experiments, stationary flying female crickets exhibit opposite reactions when exposed to pulsed sounds. To low frequency stimuli (<10 kHz), they turn their bodies as if orienting toward a calling male; to high frequency sounds (>15 kHz) they turn away as if avoiding an echolocating bat (Moiseff et al. 1978). The AN2 cell in *T. oceanicus* (and its presumed homologue in other gryllids (e.g., *Gryllus bimaculatus*, Wohlers and Huber 1978)) is a second-order, acoustically-activated interneuron whose responses to ultrasound have been described in numerous studies (for review see Pollack 1998). This cell's activity appears to be both necessary and sufficient for evoking the cricket's natural avoidance response to bat calls (Nolen and Hoy 1984).

Although it is assumed that crickets use the AN2 cell to trigger behaviours that avoid predation, only one study (Popov and Marcovich 1982) has exposed a cricket's ear to actual bat calls (see Schul et al. (2000) and Triplehorn and Yager (2002) for experiments using a bush-cricket and praying mantis, respectively). Similarly, except for anecdotal reports (Popov and Shuvalov 1977; Cranbrook and Barrett 1965), there is only one study (Bailey and Haythornthwaite 1998) that has quantitatively observed bats attacking crickets.

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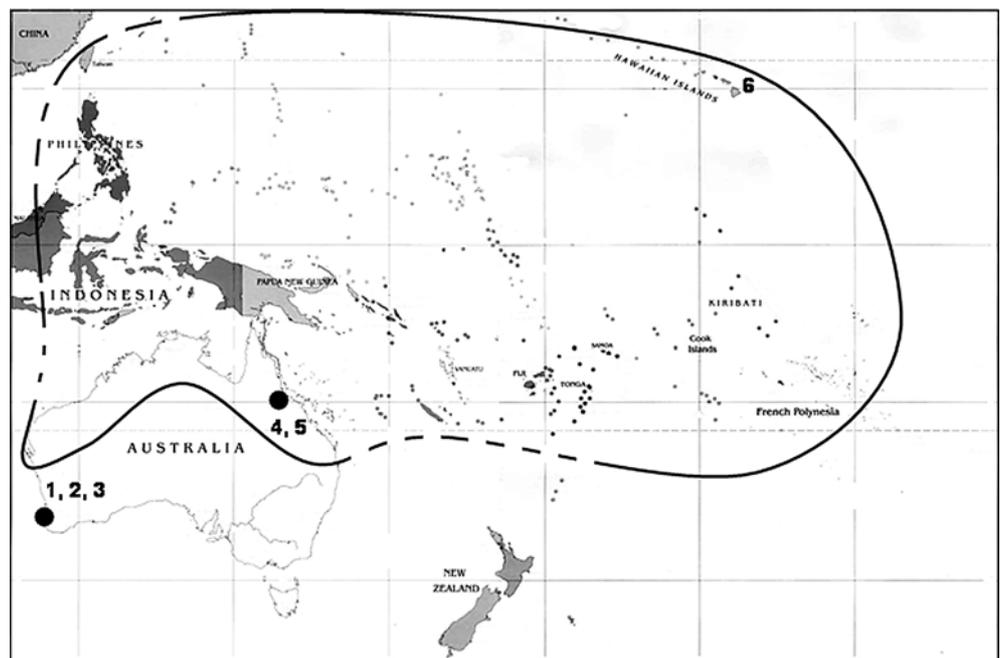
Worldwide, there are more than 700 species of echolocating insectivorous bats and the calls they emit are acoustically diverse and adapted to their varied foraging habits (Novick 1977; Simmons et al. 1979; Neuweiler 1984; Schnitzler and Kalko 2001; Siemers and Schnitzler 2004). The hunting behaviours of most insectivorous bats fall along a continuum between aerial-hawking and substrate-gleaning (Norberg and Raynor 1987; Fenton 1990). Aerial-hawking involves locating prey in flight with search calls that are typically frequency-modulated, relatively long in duration and of high intensity (Holdried and von Helverson 2003). In contrast, substrate-gleaning bats orient towards the incidental sounds generated by their substrate-bound prey and descend upon them while emitting (or not) echolocation calls that are broadband, multiharmonic and that are fainter, shorter in duration and relatively high in frequency (Neuweiler 1989; Faure et al. 1993; Arlettaz et al. 2001; Ratcliffe and Dawson 2003). The acoustic diversity of bat echolocation calls suggests that some bats may be less audible to eared prey (Novick 1977; Fenton and Fullard 1979; Faure et al. 1993; Rydell and Arlettaz 1994; Fullard and Dawson 1997). Roeder (1966) demonstrated that moths detected bats 30–40 m away rendering this sensory system an earlywarning defence. Subsequent studies on moths (for review, see Fullard 1998) suggest that some bats may be acoustically inconspicuous as a result of using frequencies mismatched (allotonic) to those at which sympatric moth ears are most sensitive. Furthermore, the short calls in the terminal phase of a bat's aerial attack echolocation sequence may not be well encoded by the moth receptor neurons (Fullard et al. 2003).

Given the Pacific distribution of *T. oceanicus* (Fig. 1), this insect is sympatric with bats using all of the afore-

mentioned echolocation/hunting strategies and should exhibit similar coevolved adaptations as that of the moth. The cricket ear, however, differs from that of the moth in possessing ~70 receptor neurons (in *Teleogryllus commodus* (Young and Ball 74)) compared to the one to four receptor-celled moth ear. This complexity allows the cricket the capability of frequency discrimination (Paton et al. 1977; Ehret et al. 1982; Faulkes and Pollack 2002) and categorical perception (Wytenbach et al. 1996). Therefore, the responses of *T. oceanicus*' AN2 cell to the pure-tone synthetic pulses used in most studies to date may not accurately reflect how the ears of this insect respond to the complex temporal and spectral structure of the echolocation calls emitted by real bats (but see Faure and Hoy 2000a for frequency-modulated stimulus pulses with the tettigoniid, *Neoconocephalus ensiger*).

In the present study, we use synthetic sounds and field recorded echolocation calls of six species of bats that are sympatric with *T. oceanicus*. We first determined whether the AN2 cell responds to the calls of bats that they would encounter under natural conditions and if these neural responses are sufficient to evoke evasive manoeuvres in a flying cricket. Second, we tested the prediction that certain bats produce search calls less conspicuous to this cricket than those of other bats. Third, we tested the prediction that the approach calls of a gleaning bat species evoke reduced AN2 responses as a potential way of increasing capture success on these insects. To interpret our results in a neuroethological context we have used the observations of Nolen and Hoy (1984) who identified a critical AN2 firing pattern in *T. oceanicus* that evokes the motor activity that underlies anti-bat avoidance behaviour.

**Fig. 1** The Pacific ocean distribution of *T. oceanicus* (excluding the Easter Islands) and the locations of the bat species whose echolocation calls were recorded for use as stimuli for the auditory preparations: 1, *Tadarida australis*; 2, *Nyctophilus geoffroyi*; 3, *Chalinolobus gouldii*; 4, *Vespadelus pumilus*; 5, *Myotis adversus*; 6, *Lasiurus cinereus*. The occurrence of this cricket in areas north and west of Australia and for most of the Pacific islands indicated is inferred (via dashed line) from collection records (Chopard 1967)



## Materials and methods

### Animals

We obtained unmated female *T. oceanicus* aged 10–15 days after their final moult from colonies maintained by Prof. Gerald Pollack (McGill University, Montréal, Canada). Insects were maintained in glass terrariums on Purina Cat Chow© and water ad libitum in environmental rooms kept at a constant 25 °C on a reversed, 12-h light, 12-h dark cycle to allow us the opportunity to experiment with the insects during their nocturnal phase.

### Electrophysiology

The large action potential generated by the AN2 cell in *Teleogryllus* spp. can be readily observed with extracellular electrodes from the exposed cervical connectives (Hill 1974; Moiseff and Hoy 1983; Samson and Pollack 2002). Crickets were cold-anaesthetized and secured, ventral side up, to a block of modelling clay. Cervical connectives were exposed by cutting a square over the neck and prothoracic sternum and the one ipsilateral to the stimulated ear was draped over a stainless-steel hook electrode that was referenced to another electrode placed in the abdomen. To reduce background neural activity the connective was severed anterior to the recording electrode and the contralateral connective was severed at its connections with the prothoracic ganglion (which leaves intact any reciprocal neural modifications between the AN1 and AN2 cells (Pollack 1998)). Neural activity was amplified with a Grass Instruments P-15 pre-amplifier, digitised at a 20 kHz sampling rate (TL-2, Axon Instruments Ltd) and stored on a PC. All records were subsequently analysed using the programme, AxoScope 8.1 (Axon Instruments Ltd).

### Acoustic stimulation—synthetic pulses

We exposed the crickets to acoustic pulses produced by a Wavetek (model 23) or Hewlett-Packard function

generator (model 3311A), shaped to a 1 ms rise/fall time (Coulbourn S84-04), amplified (National Semiconductor LM1875T) and broadcast at two pulses  $\cdot$  s<sup>-1</sup> from a Technics EAS-10TH400B loudspeaker with a flat ( $\pm$  3 dB) frequency response from 15 kHz to 70 kHz. The speaker was mounted 30 cm to insure a uniform sound field from the cricket in a sound-absorbing, foam-filled Faraday cage. Intensities were recorded as mV peak-to-peak and later converted to peak equivalent dB sound pressure level (peSPL) (rms re 20  $\mu$ Pa) from equal-amplitude continual tones using a Brüel and Kjær (B & K) type 4135 6.35 mm microphone and type 2610 B & K measuring amplifier. The system was regularly calibrated with a B & K type 4228 pistonphone. We derived auditory threshold curves (audiograms) using 20 ms pulses at 5 kHz frequency increments randomly chosen from 5 kHz to 100 kHz with threshold being determined as the dB SPL that evoked two AN2 spikes per stimulus pulse. We constructed intensity–response plots using the following durations: 1, 2, 5, 10, 20 and 50 ms and frequencies: 10, 22.5, 62.5 and 80 kHz.

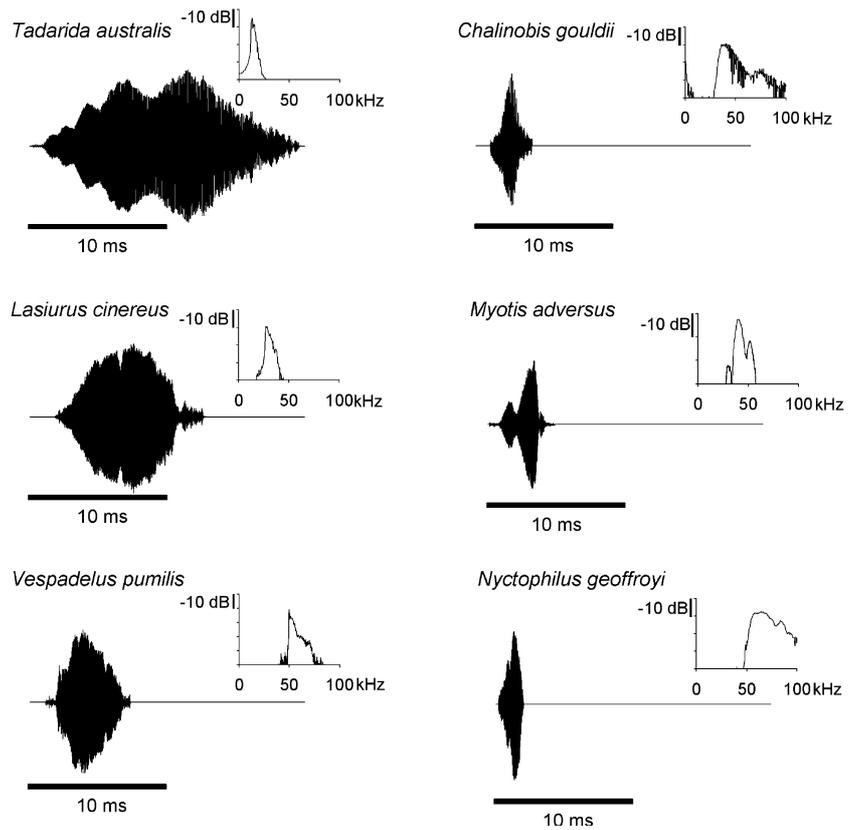
### Acoustic stimulation—bat recordings

We digitised the echolocation search calls (defined as any call preceding the approach phase with an inter-pulse interval of more than 50 ms (Griffin et al. 1960; Surlykke and Moss 2000) from the following bats that are sympatric (Churchill 1998) with the Pacific distribution of *T. oceanicus* (Table 1; Fig. 2) and recorded at the following locations (refer to citations for details of recording methods): West Australia, Australia, *Tadarida australis*, *Chalinolobus gouldii*, *Nyctophilus geoffroyi* (Fullard et al. 1991); Queensland, Australia, *Vespadelus* (= *Eptesicus* (Wilson and Reeder 1993)) *pumilus*, *Myotis adversus* (Fenton 1982; Thompson and Fenton 1982); Kaua'i, Hawai'i, *Lasiurus cinereus* (Belwood and Fullard 1984). Calls were sampled at 500 kHz with a data acquisition PCMCIA card (National Instruments DAQCard 6062E) installed in a Dell laptop computer running the program BatSound Pro (Pettersson Elektronik AB, Uppsala, Sweden) which was later used to

**Table 1** The foraging strategies of the bat species used in the playback trials and the acoustic characteristics of their echolocation search calls (see text for references to recording sites and methods)

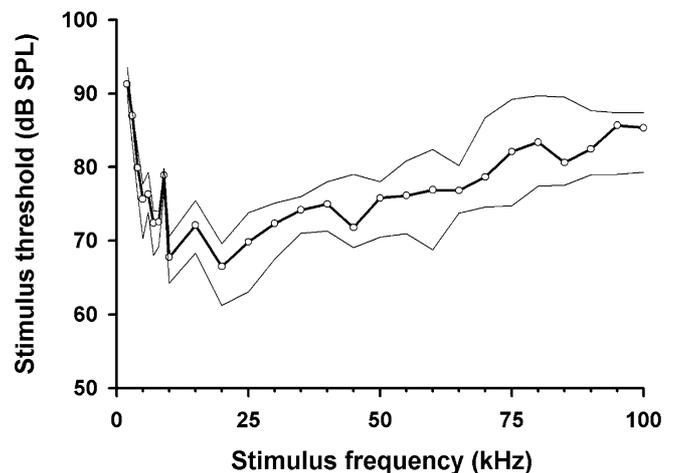
Bat species	Duration (ms)	Peak frequency (kHz)	Bandwidth (kHz)	Foraging strategy (as predicted by Norberg and Rayner 1987)
Family Molossidae				
<i>Tadarida australis</i>	18.7	12.8	16.6 (11.3–17.9)	Fast hawking, also forages on the ground
Family Vespertilionidae				
<i>Chalinolobus gouldii</i>	3.0	41.0	43.9 (32.8–76.7)	Hawking
<i>Lasiurus cinereus</i>	10.7	28.6	9.6 (26.1–35.7)	Hawking
<i>Myotis adversus</i>	3.5	40.0	10.9 (35.1–46)	Slow hawking, trawling
<i>Nyctophilus geoffroyi</i>	1.8	66.5	34.1 (54–88.1)	Gleaning, may also slow hawk
<i>Vespadelus pumilus</i>	5.5	50.1	6.2 (49.3–55.5)	Hawking

**Fig. 2** Time-amplitude patterns and frequency spectra of the search calls of the bats used in the auditory playback experiments



remove background noise (e.g., echoes, low frequency (<5 kHz) insect sounds). Calls were played back to auditory preparations of ten different individuals via the acquisition card into the same amplification and speaker system used for the pure tone pulses. To cover a range of echolocation call intensities that free-flying crickets might encounter in the wild we played back the calls at six intensities from 65 dB to 90 dB peSPL (measured at 30 cm, using a constant tone at the same peak frequency of each call (Stapells et al. 1982)). The distances from each bat that these intensities would represent depends upon the source levels of the bat (i.e., dB at 10 cm) and the effects of atmospheric attenuation (Griffin 1971; Lawrence and Simmons 1982). Bat species order and intensity were randomised for each cricket.

In addition to the search calls of these species, we exposed these same ten *T. oceanicus* auditory preparations to the attack calls of an individual *N. geoffroyi* as it approached and gleaned a fluttering moth from the fingers of a person holding the recording microphone towards the approaching bat (see Fullard et al. 1991 for recording details). As with the search calls, we played these sequences at the same range of intensities (by setting the highest amplitude pulse to the same six peSPL values as those used for search calls) to cover the range of echolocation intensities likely to be encountered by insects exposed to the attacks of gleaning bats.



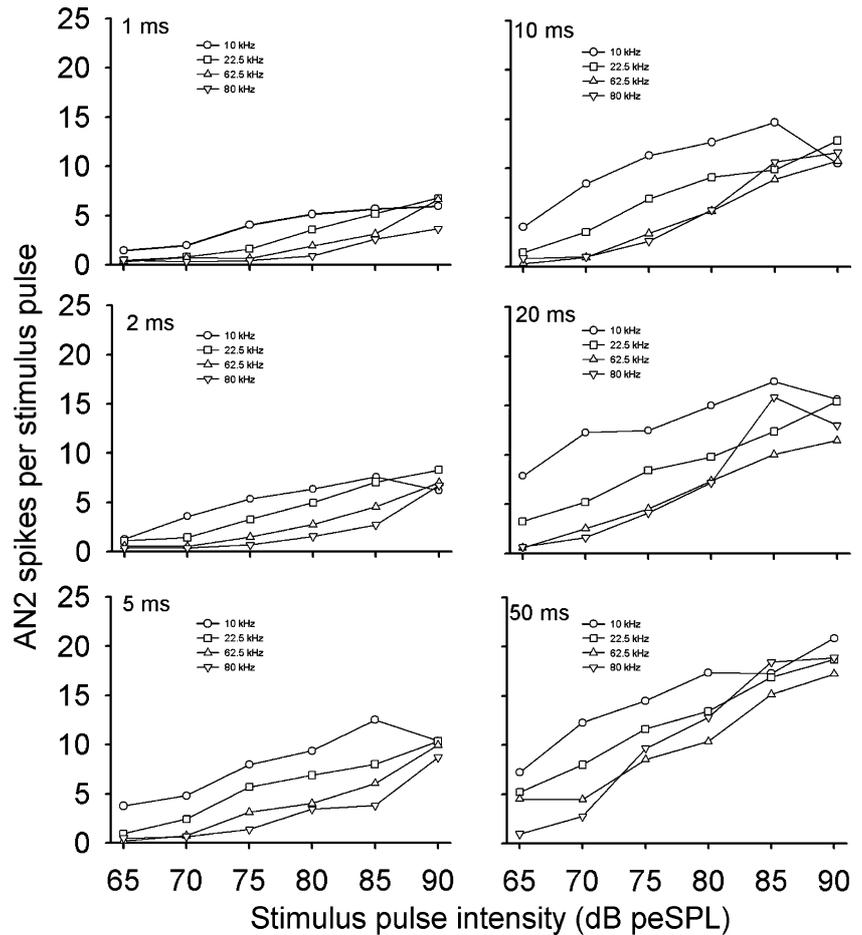
**Fig. 3** The median AN2 audiogram of 12 female *T. oceanicus* (heavy line) within the boundaries formed by the 25th and 75th quartiles (light lines)

## Results

### Auditory sensitivity

The median auditory sensitivity curve (audiogram) of 12 females, ten of which were subsequently used in the playback trials, is illustrated in Fig. 3 as a bold line bordered by the 25th and 75th quartiles of all thresholds.

**Fig. 4** Input–output curves of AN2 responses to pure tone sound bursts of varying frequencies and durations, representing the range emitted by echolocating bats. Points are of the averaged spike counts per stimulus pulse ( $n = 10$ ). The frequencies are listed to the right of each set of curves from those that are most (*top*) to least (*bottom*) detectable



In agreement with the ultrasonic portion of other neural audiograms published for *T. oceanicus* (Moiseff and Hoy 1983), our results suggest a broad tuning in the AN2 cells to ultrasonic frequencies of 10–60 kHz.

percentages of all spikes counted: 10 kHz: 0%; 22.5 kHz: 8.3%; 62.5 kHz: 27.8%; 80 kHz: 33.3%.

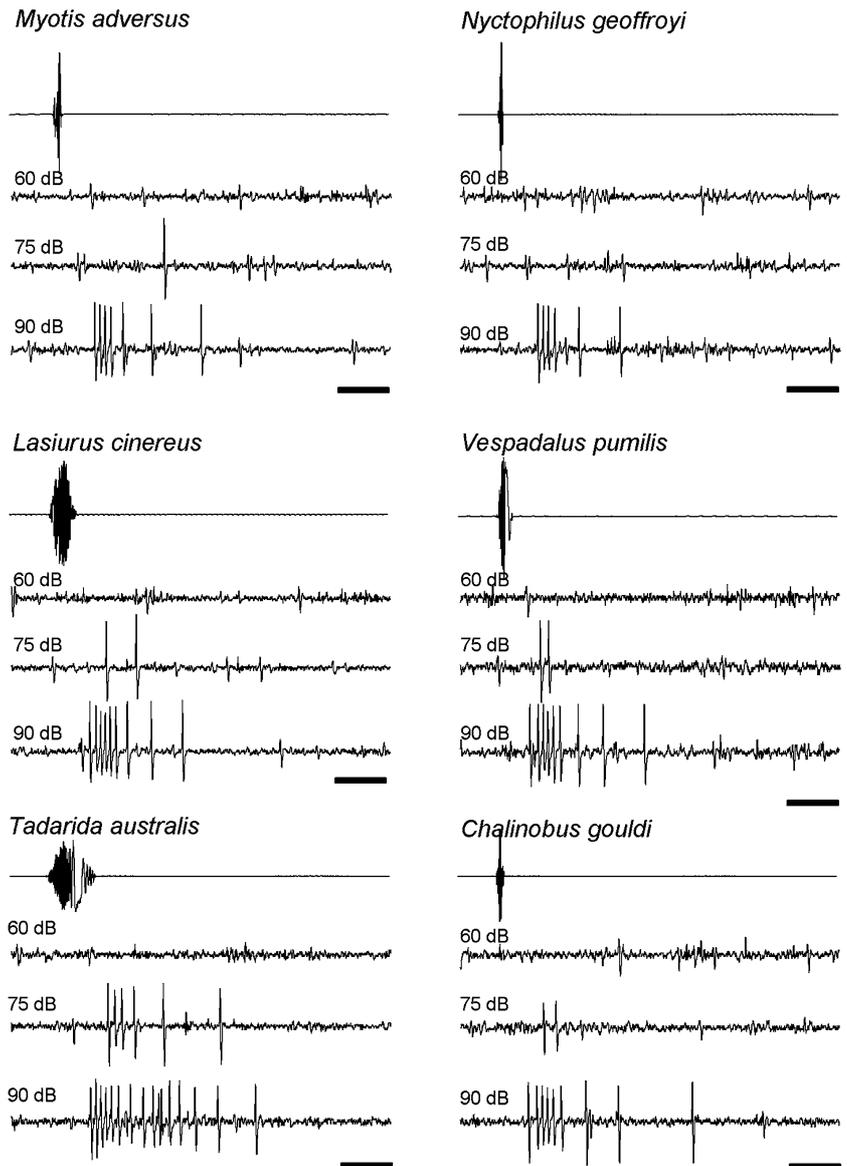
#### AN2 responses to synthetic pulses

The intensity response curves of the AN2 cell to pure-tone pulses of different frequencies and durations are illustrated in Fig. 4. The acoustic values of the pulses were chosen to simulate the predominant ranges of bat echolocation frequencies likely to be encountered by this cricket in addition to examining its responses to allo-tonic frequencies (i.e., > 60 kHz, as predicted from the audiograms of Fig. 3). As expected from these audiograms, the AN2 cell exhibits maximal firing response to 10 kHz pulses at all durations and intensities used with slight saturation (i.e., levelling off) of firing seen at 85 dB in some of the stimulus conditions. The similar median thresholds seen in Fig. 3 at 10 kHz and 22.5 kHz do not result in similar average spike counts at these frequencies with 10 kHz responses qualitatively higher at all stimulus durations. AN2-undetectable stimulus pulses (i.e., those that evoked less than one average AN2 spike per any duration pulse) occurred with the following per-

#### AN2 responses to echolocation calls

AN2 activity to these stimuli (Table 1; Fig. 2) was tabulated as the average number of spikes ( $n = 10$  animals) per stimulus pulse and the instantaneous period (IP) of the spikes (i.e., the time (ms) from the start of one spike to the other). We follow the arguments of Fullard et al. (2003) and Nabatiyan et al. (2003) that contend that it is neural spike IPs combined with total spike number that determine the tendency to fire in postsynaptic cells and are a more realistic predictor of a neuron's contribution to evoked behaviour than traditional averaged rate measurements of firing activity (e.g., spikes/sec). We caution that in reading the graphs in Figs. 7 and 9, this measurement is the reciprocal of rate and high IPs actually indicate low responsiveness. We chose to use the recordings of bats that represent species sympatric with *T. oceanicus* in their native habitats (Fig. 1) and possess a range of echolocation parameters (Table 1). Although the recordings made in Western Australia were from bats approximately 1,000 km south of the distributional limit of *T. oceanicus* (Otte and Alexander 1983), the

**Fig. 5** Representative traces of AN2 responses to the search call of the bats used in the playback experiments at 60, 70 and 90 dB peSPL (at 30 cm). Scale bar for each trace, 20 ms. The apparent amplitude modulations seen in some of the bat calls are due to the insufficient digital sampling used in creating the figure, but were not present in the stimuli used for the auditory trials

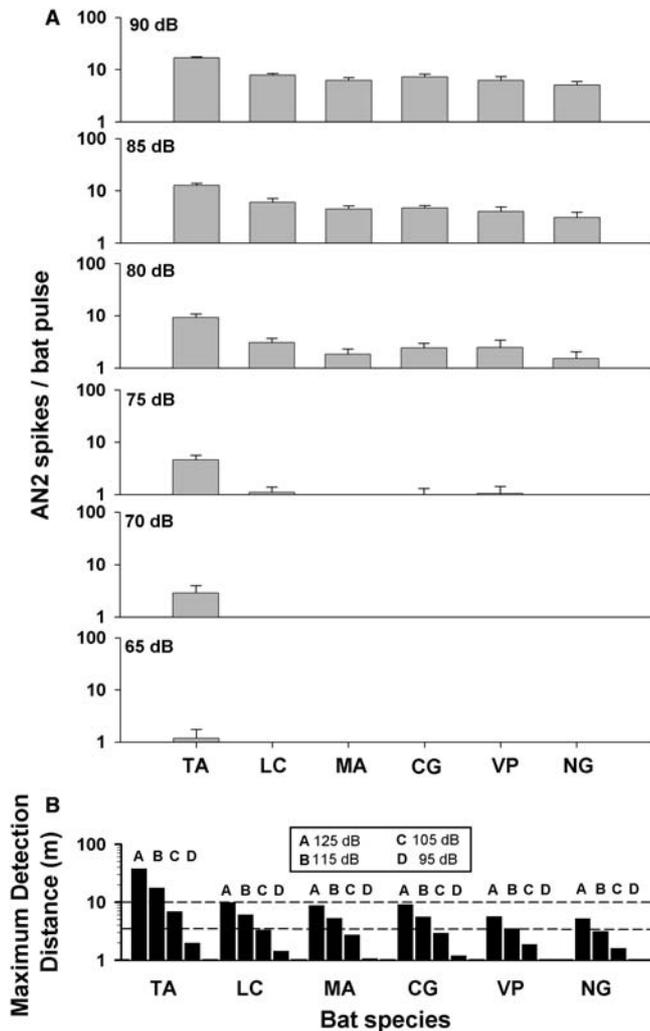


Australian distributions (Churchill 1998) of all of these bats extend well into that of *T. oceanicus* and we assume that the echolocation calls of the bats we recorded do not differ substantially from their northern conspecifics (but see Law et al. 2002).

#### Search calls

There are distinct differences in the AN2 responses to the search calls of the six species of bats that were used as acoustic stimuli (Figs. 5-7). The long, low frequency calls of *Tadarida australis* evoked more AN2 spikes per call than any other bat at any intensity used (Fig. 6) while the short, high frequency calls of *N. geoffroyi* elicited the fewest. Using the AN2 thresholds as described in the audiograms of Fig. 3 and the peak frequencies of each bat (Table 1), Fig. 6b illustrates the estimated distances given an atmospheric humidity of

50% (Griffin 1971; Fenton and Fullard 1979; Moiseff and Hoy 1983) that the AN2 cell would first begin to respond at four different source level intensities that cover the range of those reported for aerially hawking bats (Waters and Jones 1995; Jensen and Miller 1999; Boonman and Jones 2002). Source levels are used in these calculations since it is the attenuation from the emitted intensities of the bats that determine the detection distances that the auditory thresholds of the cricket AN2 cells produce. Figure 6b predicts that for calls emitted at 125 dB, all of the bats would activate the AN2 cell before the bat has approached to 3.5–10 m from the cricket, the distances estimated at which an aerially hawking bat detects the echoes from its calls (Kick 1982; Jensen and Miller 1999; but see much higher theoretical distances reported by Holderied and von Helversen 2003). For lower source levels the calls of *T. australis*, *L. cinereus*, *M. adversus* and *C. gouldii* will continue to evoke strong AN2 responses while



**Fig. 6** **a** AN2 spike number responses ( $n=10$  animals) to the search calls of the bats played at different intensities, bats: *TA* *Tadarida australis*; *LC* *Lasiurus cinereus*; *MA* *Myotis adversus*; *CG* *Chalinolobus gouldii*; *VP* *Vespertilio pumilus*; *NG* *Nyctophilus geoffroyi*. **b** Calculated maximum distances that the AN2 would first begin to fire from the bats assuming four different initial source level intensities (dB at 10 cm), dashed lines indicate the range of distances that bats were estimated to respond to the echoes of their prey targets

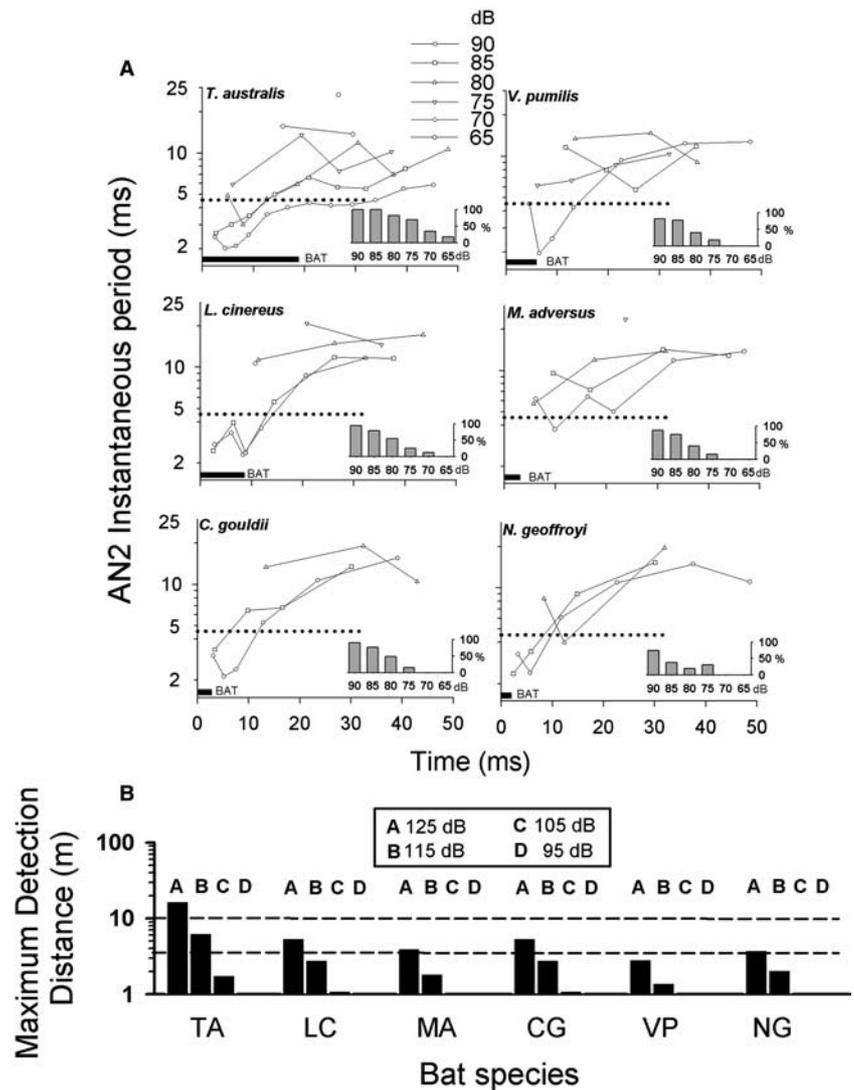
those of *V. pumilus* and *N. geoffroyi* no longer activate the AN2 cell responses at this critical distance at source levels of less than 115 dB. Of all the bat calls tested, those of *N. geoffroyi* evoked the least overall AN2 response and would only be detectable above the 3.5 – 10 m critical distance if this bat was echolocating at a source level intensity above 125 dB, values unlikely in gleaning bats (Faure et al. 1990, 1993; Waters and Jones 1995; Boonman and Jones 2002). The foraging strategy of gleaners however suggests that this bat preys primarily upon non-flying insects and its detectability would be relevant only to a substrate-bound (i.e., walking) cricket. We examine the responses to the gleaning attack sequence of this bat in the next section.

The bat detection distances predicted from the simple appearance of AN2 spikes are less if one examines this cell's IPs to the calls (Fig. 7). These graphs illustrate that the AN2 IP increases (i.e., its firing rate decreases) during its response to an echolocation call and that this reduction in firing varies to different bats. Using the criterion of Nolen and Hoy (1984) of 4.54 ms as the critical AN2 IP for evoking abdominal avoidance movements, it can be seen that the calls of all bat species delivered at 90 dB initially evoke IPs below 4.54 ms but quickly increase above this value. For bat calls played at 90 dB from *T. australis* and *L. cinereus*, AN2 IPs remain below 4.54 ms throughout the time the call is presented. For the other bats, however, this critical IP is expressed only for the first one or two spikes and for bats such as *M. adversus* only a few responses at 90 dB ever evoke IPs sufficiently short to predict they will elicit avoidance flight movements. In addition, the percent of animals that do not respond at all to the calls increases as the intensities of the calls decrease to the point where 50% of the crickets fail to respond to all bat calls except for those of *T. australis* at intensities of less than 80 dB. Figure 7B predicts the maximum distance that the search calls of the bats would evoke 4.54 ms IPs for each of the bat calls used in the playbacks at four different source level intensities. As with the results using the initial appearance of AN2 spikes (Fig. 6b), the calls of *T. australis*, *L. cinereus* and *C. gouldii* will evoke behaviourally significant AN2 IPs before the distance at which the bats would be aware of the cricket's echo but *M. adversus* joins *N. geoffroyi* and *V. pumilus* in not eliciting AN2 responses until they are closer than 3.5 m at the highest source level used.

#### Gleaning attack calls

Figure 8 shows a cricket's AN2 response to the pre-recorded gleaner echolocation sequence of *N. geoffroyi* as it approached and captured a fluttering insect (Fullard et al. 1991). As is typical with *Nyctophilus* spp. this bat does not emit a terminal feeding buzz and often ceases echolocating completely as it approaches its target (Grant 1991; Bailey and Haythornthwaite 1998; but see Ratcliffe et al. 2005 for an alternative explanation of call cessation in gleaner bats). In our case, the bat maintained its echolocation search calls but did not emit a feeding buzz when it captured its prey. As can be seen from the neural trace, the AN2 cell responded with increased firing at the highest intensity tested but only at a point approximately 200 ms before the bat would have contacted the cricket. To track the AN2 responses to this attack sequence, we analysed both average spike numbers and IPs as they occurred in 50 ms bins during the entire time that ten crickets were exposed to the sequence (Fig. 9). These peri-stimulus histograms were computed for the different intensities that the sequences were played at and show that to the gleaner attack of *N. geoffroyi*, the AN2 illustrates an extremely reduced

**Fig. 7 a** Average AN2 instantaneous firing periods ( $n = 10$  animals) to playbacks of bat calls at different intensities. (Inset, average percent probability of the AN2 cell to fire at least five times in all crickets at all intensities). Horizontal dotted lines indicate interspike interval of 4.5 ms (see text). **b** Calculated maximum distances that the AN2 would fire at the critical period of 4.54 ms from the bats assuming four different source level intensities, *dashed lines* indicate the range of distances that bats first respond to the echoes of their prey targets



response to this bat's calls. Even at the playback's highest intensity (90 dB), AN2 spike numbers are erratic and average IPs rarely attain Nolen and Hoy's (1984) critical value of 4.54 ms throughout the duration of the sequence. Individual responses did, however, occasionally reach this critical IP value (65 dB: 0%; 70 dB: 4.9%; 75 dB: 0%; 80 dB: 8.9%; 85 dB: 22.1%; 90 dB: 36.5%).

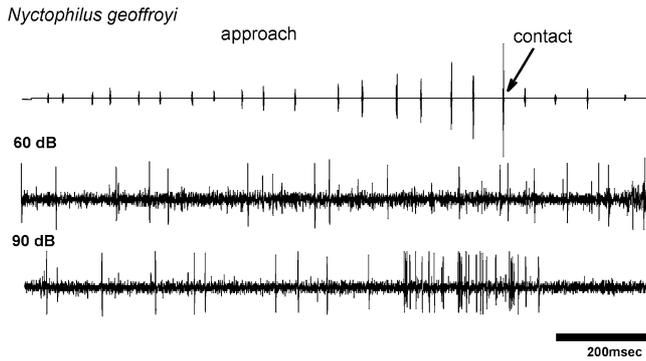
## Discussion

The initial detection of a bat's echolocation call by an eared insect is influenced primarily by three acoustic variables: frequency, duration, and intensity. In addition, the repetition rate of pulses increases as the bat enters the final phase of its attack (Griffin 1958; Kick and Simmons 1984) and can theoretically cue the insect to the proximity of the bat (Miller and Olesen 1979; Fullard 1984). In contrast to the constant nature of these variables in the stimuli used in most auditory

physiological studies, real bats manipulate all of them simultaneously as they hunt (Surlykke and Moss 2000). We believe that the use of biological stimuli in the form of actual bat calls can provide testable predictions regarding the sensory ecology and evolutionary history of this cricket's relationship with its bat predators. We further recognize the possibility that other components of the cricket auditory processing pathway (e.g., AN1 (Poulet and Hedwig 2003)) may ultimately prove to influence the final behavioural output of this insect's flight response to bats.

## Frequency

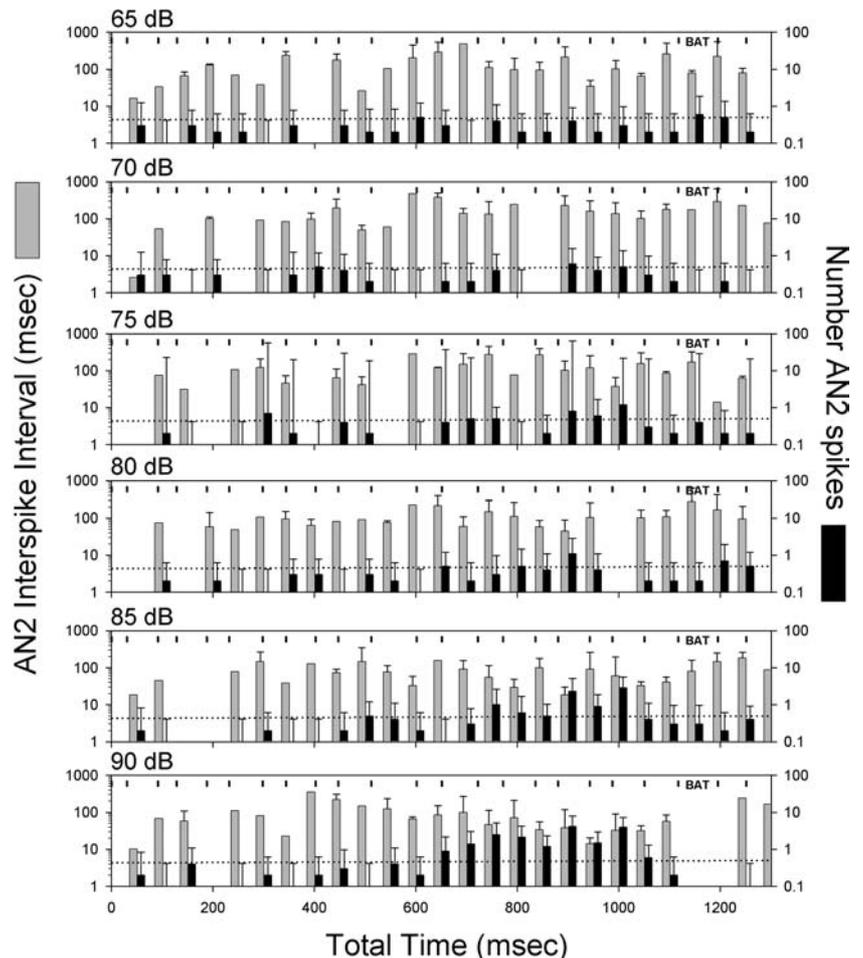
The audiograms from this study and previous studies (Moiseff and Hoy 1983; Nolen and Hoy 1986) indicate that the ultrasound sensitivity of AN2 in *T. oceanicus* is broadly tuned to frequencies of 10–60 kHz, the bandwidth emitted by most insectivorous echolocating bats and suggest that these bats and their echolocation



**Fig. 8** Representative traces of AN2 responses to the gleaning attack calls of *N. geoffroyi*

frequencies have imparted the greatest selection pressure on this neuron's physiological design in the same fashion as that argued for the auditory receptors of moth ears (Fullard 1988). Our observation of a relatively flat AN2 audiogram in *T. oceanicus* compared to a sample of North American moths (Surlykke et al. 1999) may reflect this tropical cricket's coevolution with a more diverse assemblage of bats and their echolocation frequencies (Fullard 1982).

**Fig. 9** Average AN2 responses (interspike interval and total number of spikes per 50 ms bin width,  $n=10$  animals)) to the gleaning attack echolocation sequence of *N. geoffroyi* (individual pulses indicated as vertical lines) delivered at different intensities. Horizontal dotted line indicates interspike interval of 4.5 ms (i.e., the critical AN2 firing rate (220 Hz) required for avoidance movements (Nolen and Hoy 1984))



As well as indicating which bats have influenced the sensitivity of the *T. oceanicus* AN2, the audiograms also predict that bats echolocating with allotonic frequencies to those of the AN2 cell's sensitivity will evoke reduced defensive reactions in the cricket. Allotonic echolocation was proposed as a counter-manoeuvre by bats against the eared defences of insects (Novick 1977; Fenton and Fullard 1979; Fullard 1988) and most studies on the diets of these bats now support this theory (Jones 1992; Rydell and Arlettaz 1994; Pavey and Burwell 1998; Bogdanowicz et al. 1999; Jacobs 2000; Jones and Waters 2000; Leslie and Clark 2002; but see Guillen et al. 2000). Allotonic bats theoretically exist either above a prey's auditory best frequency (e.g., *Cloeotis percivali*: 212 kHz (Fenton and Bell 1981)) or below it (e.g., *Euderma maculatum*: 12.4 kHz (Fullard and Dawson 1997); *Tadarida teniotis*: 11–12 kHz (Rydell and Arlettaz 1994)). At the high spectral end of the bats in the present study, the 65+ kHz calls of *N. geoffroyi* evoked the least AN2 responses suggesting that its high frequency, short duration echolocation calls may be inconspicuous while gleaning when calls may be produced at lower intensities than while aerially hawking (Faure et al. 1993; Schnitzler and Kalko 2001). Bailey and Haythornthwaite (1998) showed that this bat preys successfully on singing,

unconcealed *T. oceanicus* implying that crickets do not detect this bat while it is searching for prey. Extremely high frequency bats (>140 kHz), some of which feed heavily upon eared moths (e.g., *Hipposideros ater* (Pavey and Burwell 1998)), are also sympatric with the Australian distribution of *T. oceanicus* and allotonicity could function in these bats' ability to prey upon crickets. This hypothesis is supported by the observations of Popov and Markovich (1982) that the 92 kHz calls of *Rhinolophus blasi* elicited no responses in the putative AN2 homologue in *G. bimaculatus* under laboratory conditions. Interestingly, *R. blasi* both gleans and hawks its insect prey (Siemers and Ivanova 2004).

While high frequency allotonicity may exist in certain bats that hunt *T. oceanicus*, the option for low frequency inconspicuousness does not appear available since the AN2 cell possesses good low frequency sensitivity (perhaps as a derivation of its use in responding to calling songs (Hutchings and Lewis 1984)). We suggest, however, that very low frequency bats such as *T. australis* could use their calls in another fashion to increase their predatory success on crickets. Depending upon stimulus pulse rate and intensity, tethered flying *Teleogryllus* spp. will either orient away from or towards pulsed tones of 10–15 kHz (Moiseff et al. 1978; Pollack et al. 1984; Nolen and Hoy 1986). From these studies, we suggest that a hunting *T. australis*, echolocating with 12 kHz pulses emitted at rates approximating those of calling crickets (e.g., 10–20 pulses/s (Otte and Alexander 1983)) might evoke ambiguous flight reactions in the cricket that would allow the bat to approach within echo-detection distance. If true, this would represent a novel case of predatory sensory exploitation (Haynes and Yeargan 1999) since the bat would be exploiting the normal positive phonotaxis of female crickets as they search for singing males.

#### Duration

As illustrated in Fig. 4 and other studies (Moiseff and Hoy 1983), the AN2 cell encodes stimulus duration with little evidence of saturation up to intensities of 100 dB and exhibits considerable after-firing to short pulses. The AN2 cell, however, rapidly adapts to continual sounds (Moiseff and Hoy 1983) and using the 4.54 ms IP threshold criterion of Nolen and Hoy (1984), our results predict that only the first 1–2 ms of a stimulus pulse would evoke a turning response in a free-flying cricket. Similar tuning to short signals has also been reported for the T-cell in the tettigoniids, *Tettigonia viridissima* (Rheinlaender et al. 1972) and *Neoconcephalus ensiger* (Faure and Hoy 2000a), a characteristic which may differentiate these anti-predator interneurons from those involved in mate-detection. The spike responses of AN2 to the relatively long search calls of *T. australis* (Fig. 6) predicts that this bat will evoke behaviourally supra-threshold responses in *T. oceanicus* at distances greater than 10 m, in contrast to the 4–5 m response distance

predicted in Nolen and Hoy (1986). The shorter calls of *C. gouldii* and *V. pumilus*, although syntonetic and capable of evoking numerous AN2 spikes, will elicit turning (i.e., evoke short enough IPs) only at intensities greater than 85 dB. The calls of *M. adversus* appear even less detectable, evoking critical AN2 IPs only at dBs of 90 and higher. This last result is surprising given that the calls of *M. adversus* used in this study were longer than those of *C. gouldii* although the peak frequencies were similar (Table 1) and we suggest that this indicates the potential importance of call bandwidth for the detection of bats by crickets. The search calls for *C. gouldii* were more than 30 kHz (at –15 dB from peak frequency) broader than those of *M. adversus* (Table 1) and contain more energy at higher frequencies. We suggest that this sound energy would activate a greater number of high frequency auditory receptors (Imaizumi and Pollack 1999) enabling the AN2 to respond to the otherwise shorter calls of *C. gouldii*. Recently, Seimers and Schnitzler (2004) showed that bandwidth (especially the upper range) was of importance for bats that hunt in cluttered environments. Our study provides evidence that the frequency-discriminating ears of crickets may be better able to detect the broad bandwidth calls of clutter-hunting bats by dedicating certain sensitive neurons to only detecting high frequencies than the one to four auditory receptors found in tone-deaf insects such as moths (Fenton and Ratcliffe 2004).

#### Intensity

Least understood of all the echolocation parameters is the emitted intensity of the calls, a situation caused by the rapidly changing orientation of the bat and its head as it flies towards the recording microphone combined with the tendency of bats to alter their intensities in different environments (Griffin 1958; Surlykke et al. 1993; Valentine et al. 2002; Ghose and Moss 2003)). For this reason, we exposed the AN2 cell to intensities that should cover the range of those naturally encountered by a flying cricket. As expected, the more intense a bat's echolocation call, the further away it will evoke AN2 responses that should trigger avoidance flights (Figs. 6, 7) and most bats emitting calls with source levels in excess of 115 dB will not be able to approach the cricket to within the 3.5–10 m echo detection distance required by the bats before the cricket turns away. Our maximum response distances estimated from the first appearance of AN2 spikes (Fig. 6b) are in better agreement with the behavioural experiments of Nolen and Hoy (1986) than with those computed using Nolen and Hoy's (1984) AN2 IP as the critical determinant of *T. oceanicus*' avoidance behaviour (Fig. 7b). This suggests that the AN2 IP of 4.54 ms may be a conservative indicator of the beginning of an avoidance response (e.g., Pollack (1998) uses an IP of 5.6 ms (180 Hz) as a threshold). Additionally, abdominal movements may not be the first or only physical reaction of flying *T. oceanicus* to distant

bats indicating avoidance manoeuvres. Changes in wing movements in these insects have not yet received the examinations of high resolution film or videographic observation techniques (e.g., Dawson et al. 1997; Berger and Kutsch 2003) that may reveal responses that would allow the cricket an earlier chance of avoiding bats.

The critical component of these predictions is the natural echolocation intensity of aerially hawking bats with estimates of the source levels of bats ranging as high as 133 dB (Holderied and von Helversen 2003). For an eared insect, the best encounter with a bat would occur in an open habitat since the high echolocation intensities of aerial-hawking bats will provide the furthest “early warning” cues for the insect. Nolen and Hoy (1986), using a range of frequencies and a source level of 110 dB (which may be too low for most aerially foraging bats), estimated that the AN2 cell of *T. oceanicus* and *T. commodus* would first detect bats at distances of 3–20 m. Our estimates using a higher source level of 125 dB improve the crickets’ chances by increasing their bat detection distances while providing faces to the theoretical echolocation calls (e.g., at 125 dB, *V. pumilis*: 5.9 m; *T. australis*: 39.6 m). Using the behavioural thresholds measured from Nolen and Hoy’s (1984) AN2 IP of 4.54 ms these distances shrink to 2.9 and 17.1 m, respectively, but should still allow the cricket sufficient time to escape most of the aerially hawking bats it encounters. Similar values to these can be estimated from behavioural responses and neural thresholds of ultrasonically sensitive interneurons in tettigoniids (Libersat and Hoy 1991; Shul et al. 2000; Faure and Hoy 2000b).

#### Aerial attack calls

Once an aerially hawking bat has locked onto its target, it changes its echolocation calls from relatively long durations and periods to shorter, more rapidly repeated pulses (the “terminal” phase (Griffin et al. 1960; Simmons et al. 1979; Surlykke and Moss 2000)). This presents a considerably different problem for a fleeing insect since the bat, now possessing an echo of the target’s position, will actively follow the insect as it manoeuvres away from it. For moths, this change in the bat’s hunting strategy evokes a switch from controlled avoidance “far-bat” flight to erratic, protean “near-bat” flight that presumably increases the unpredictability of its position as the bat closes (Roeder 1967, 1975). This “bimodal” behaviour was hypothesized by Roeder (1974) to be governed by the activity of a second auditory receptor, the A2 cell. Observations of the near-bat response in one-celled notodontid ears (Surlykke 1984) however, suggests that the increased firing of a single receptor cell combined with short IPs may be sufficient to evoke this behaviour (Fullard et al. 2003). As with moths, tethered *T. oceanicus* exhibit directional flight away from faint ultrasonic pulses and non-directional body motions to intense stimuli (Nolen and Hoy 1986)

that would presumably cause it to fly erratically. It appears therefore, that *T. oceanicus* also possess a bimodal anti-bat response controlled solely by changes in the AN2 firing patterns.

#### Gleaning attack calls

A gleaning bat locates its substrate-bound target by exploiting the sounds produced by its intended prey (Anderson and Racey 1993; Arlettaz et al. 2001) and/or by using echolocation (Schmidt et al. 2000; Ratcliffe and Dawson 2003). The echolocation sounds emitted by most gleaning bats are low in duty cycle, of low intensities and of short durations and broadband frequency structure (Neuweiler 1989), characteristics usually attributed to the bats’ perceptual requirements of hunting in closed, acoustically cluttered environments (Schnitzler and Kalko 2001). Adding to the physical benefits of these types of echolocation calls is the fact that eared prey will find these calls more difficult to detect, allowing a gleaning bat to fly closer before the insect initiates a defensive response (Fullard 1987). Even though a relatively high percentage of spike pairs exhibit IPs below the critical flight value of 4.52 ms to the gleaning attack calls of *N. geoffroyi* at 85 and 90 dB, the point at which the AN2 appears to begin to respond, suggests that once a cricket detects the bat, it would be too late to escape from it.

An important point is, of what relevance are AN2 firing patterns for flight responses to a substrate-bound cricket under threat from gleaning bats? Pollack et al (1984) observed that female *T. oceanicus* walk away from high frequency sounds and it is possible that non-flying females use an active AN2-evoked defence to seek refuges when gleaning bats are present, however we do not know what, if any, AN2 firing pattern releases this avoidance behaviour. While true gleaning involves taking substrate-bound prey, the flexibility of hunting strategies in these bats indicates that some will also attack flying insects (Ratcliffe and Dawson 2003). Insects that fly close to the vegetation (e.g., as they feed from flowers) could face predation from gleaners and could actively defend themselves by dropping when they hear a bat approach (Roeder et al. 1968; Göpfert and Waserthal 1999). If gleaners represent a sufficiently high percentage of the bats in a community, it would be expected that insects will have defences against them but these could be exclusively passive (e.g., restricting sound-producing activities to concealed locations (Bailey and Haythornthwaite 1998)). Ultrasound-deaf, Neotropical frogs (*Smilisca sila*) call at night near waterfalls presumably to acoustically mask themselves from gleaning bats (Tuttle and Ryan 1982): animals do not have to actively detect predators to defend themselves against them. The behavioural responses of free-moving insects to the natural gleaning behaviour of bats has received relatively little attention and considering the probably underestimated abundance of these bats

represents a new field of study in the expanding knowledge of insect auditory-evoked anti-predator behaviour.

In conclusion we believe that the cricket AN2 neural response data provides sufficient evidence to predict that this insect will escape predation from most aerially foraging bats; but as with moths, there are certain echolocation and hunting strategies that can allow the bats that use them to increase their ability to prey upon them. The ultimate test of these predictions will come when the behavioural responses of wild crickets to free-flying bats that use these different strategies can be observed.

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