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INTENSITY RESPONSES OF THE SINGLE AUDITORY RECEPTOR OF NOTODONTID MOTHS: A TEST OF THE PERIPHERAL INTERACTION HYPOTHESIS IN MOTH EARS

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Summary

It has been proposed that the most sensitive auditory receptor cell (A1) in the two-celled ears of certain noctuoid moths is inhibited by its partner, the A2 cell, at high stimulus intensities. We used the single-celled ears of notodontid moths, also noctuoids, to test this hypothesis. The A1 cells of all but one of the moths tested exhibited non-monotonic firing rates, with reduced firing rates at high stimulus intensities and showing no relationship to the firing rate of the only other receptor, the non-auditory B cell. These results challenge the peripheral interaction hypothesis for A1 firing patterns in two-celled moth ears. An examination of notodontid A1 adaptation rates and laser vibrometry results suggests that receptor adaptation and tympanal motion non-linearity are more likely explanations for the non-monotonic receptor firing observed in both single- and multi-celled moth ears.

Key words: notodontid, moth, intensity response, auditory receptor cell, peripheral interaction, hearing.

Introduction

Noctuoid moths possess simple ears consisting of a tympanic membrane serviced by one (in the Notodontidae) or two (in the Noctuidae, Arctiidae, etc.) auditory receptor cells (A1 and A2) that allow the moths to detect the echolocation calls of aerially hunting bats (Roeder, 1967, 1974) and, in exceptional cases, the social signals of conspecifics (Alcock and Bailey, 1995; Conner, 1987; Spangler, 1988; Sanderford *et al.* 1998). In two-celled ears, the thresholds of the A1 cell are 20–30 dB SPL lower than those of the A2 cell, differences that supposedly provide the moths with the ability to discriminate between far and near bats (Roeder, 1974). Coro and Pérez (1983, 1984) observed that only the A1 cell of the arctiid *Empyreuma pugione* (=*affinis*) exhibits a non-monotonic firing response to increasing stimulus intensities, reaching a maximum firing rate at approximately 55 dB (approximately +20 dB re threshold of the A1 cell) and showing a reduced rate in response to more intense stimuli. They noted that this response curve inversely mirrored that of the A2 cell, and postulated that the A2 cell, when activated, inhibits the A1 cell, possibly *via* GABAergic chemical synapses (Pérez and Coro, 1986*a*). Since not all the species they tested exhibited non-monotonic firing responses, Pérez and Coro (1986*b*) later postulated that two types of ears exist in noctuoids, a surprising possibility for such closely related insects. As alternative explanations for these A1 responses, Coro and Pérez (1983) suggested that A1 drop-off at high stimulus intensities might arise either from non-linear motion of the tympanic membrane or from receptor fatigue, but rejected these hypotheses. The existence of peripheral intercellular communication within the simple neural organization of the moth ear seems doubtful. The few morphological cellular examinations that have been made of noctuoid auditory receptors (Ghiradella, 1971; Surlykke, 1984) reveal no evidence of any collateral plexus such as that purportedly governing intercellular communication in the fly *Drosophila melanogaster* (Shanbhag *et al.* 1992).

Notodontid moths differ from other noctuoids in that their metathoracic ears contain only one auditory receptor, the A1 cell (Eggers, 1919; Fullard, 1984; Surlykke, 1984). Since there is no A2 cell in these moths, the intensity–response curves of their A1 cell can provide a natural test of the peripheral interaction hypothesis of Coro and Pérez (1983).

Materials and methods

Animals

We used the ears of four species of notodontid moths captured from wild populations at the Queen's University Biological Station in eastern Ontario, Canada, *Datana ministra* (Drury), *Schizura leptinoides* (Grote) , *Heterocampa biundata*

(Walker), *Peridea ferruginea* (Packard), and two species collected near Odense University on the island of Fyn in Denmark, *Pheosia gnoma* (F.) and *Ph. tremula* (Cl).

Auditory analyses

The auditory nerves of the Canadian moths were exposed while positioned ventrum-up to ensure maximal exposure of their ventrally directed tympanic membranes. Auditory receptor responses were recorded extracellularly using standard electrophysiological techniques (Fullard *et al.* 1997). Stimuli were chosen to reflect those used by Coro and Pérez (1983, 1984), consisting of 45 ms pulses at 35 kHz with 1 ms rise/fall times generated by a Wavetek function generator (model 23), shaped to a 1 ms rise/fall time (Coulbourn S84-04), amplified (National Semiconductor LM1875T) and broadcast at 1 Hz from a Technics EAS-10TH400B loudspeaker with a flat (±2 dB) frequency response from 15 to 70 kHz mounted 30 cm from the moth. Intensities were recorded as mV peak-to-peak and later converted to dB SPL (rms re 20 μPa) from equal-amplitude continual tones using a Brüel and Kjær (B&K) type 4135 1/4 inch (6.35 mm) microphone and type 2610 B&K measuring amplifier following calibration with a B&K type 4228 pistonphone. Receptor responses were tabulated in the fashion suggested by Coro and Pérez (1983) by using the total number of action potentials per stimulus pulse to compute the 'total discharge frequency' and the number of receptor spikes occurring within the middle 10–40 ms of the stimulus pulse to compute the 'effective discharge frequency'. We also recorded receptor afterdischarge (Pérez and Coro, 1986*b*), the number of spikes occurring up to 50 ms after the stimulus pulse ended, and the discharges of the spontaneous, non-auditory B cell (easily distinguished by its regularity, different spike height and shape; Fig. 1) during bouts of acoustic stimulation.

Tympanal vibration

Tympanal responses to acoustic stimulation were observed in the Danish notodontids, *Pheosia tremula* (*N*=4) and *Ph. gnoma* (*N*=4), using a Dantec laser vibrometer (model GL G53650). The general principles for laser vibrometry have been described previously (Michelsen and Larsen, 1978). The abdomen of the moth was removed so that the laser beam could be directed perpendicularly onto the tympanic membrane, situated dorsally on the caudal part of the thorax. The laser was focused on the central part of the tympanum where the A1 receptor attaches (Surlykke, 1984). Control measurements were made by focusing the laser on the cuticle surrounding the ear. The stimuli were 5 ms broadband frequency sweeps from 1 kHz to 100 kHz generated by a dynamic signal analyzer (HP3562A), power-amplified (Xelex type DD10-P9), and broadcast from a Technics EAS-10TH400B leaf tweeter. Although these stimuli differ from those used for the auditory analyses, they are consistent with the techniques required for vibrational studies. The output of the speaker was linear, with a driving voltage up to at least 110 dB SPL. The loudspeaker was placed 50 cm from the moth's ear, and the stimulus intensity at the preparation was varied from 72 to 108 dB SPL in 6 dB steps. The laser vibration signal was fed into the signal analyzer (HP3562A) to generate transfer functions for phase and amplitude. Transfer functions were averaged over 10 stimuli. The vibration velocities at different stimulus intensities were determined at 45 kHz, the best frequency (measured empirically) of the ears of both species (Surlykke, 1984; A. Surlykke, unpublished data).

Results

Auditory analyses

The auditory responses of the notodontids were one-celled even in response to the highest intensities tested (Fig. 1). Every individual tested except one (SL0143) exhibited non-monotonic response curves and afterdischarge drop-off in response to increasing stimulus intensity (Fig. 2). Maximum A1 firing rates occurred at 70–80 dB and were reduced at the highest intensity tested by 20.9±5.2 % (total discharge frequency) and 23.5±5.0 % (effective discharge frequency) (means ± 1 S.E.M.). In addition, every individual except one (SL0143) showed a sharp reduction in the number of afterdischarge receptor spikes, with a mean percentage decrease of 42.9±7.9 % and a significant correlation between the percentage decrease in total and effective discharge frequency and the percentage decrease in the afterdischarge for all individuals tested (Spearman rank correlation: r_S=0.63, P=0.028, N=12). One specimen of *S. leptinoides* (SL0143) had an unusually high A1 threshold; thus, it was not possible to stimulate this preparation with more than approximately +30 dB re threshold. We measured potential acoustic responses of the B cell by comparing the mean discharge rates of this spontaneously firing cell at stimulus intensities of 45–70 dB with those at 75–100/105 dB. The ratio of B cell firing rates increased in seven of the 12 specimens tested (3.1±0.9) and decreased in the other five (0.8±0.1) (means ± 1 S.E.M.), with no significant correlation between the change in B cell

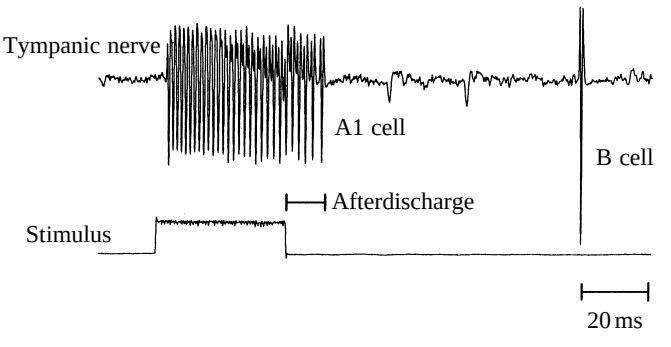

Fig. 1. A representative trace of the receptor response to a 45 ms, 30 kHz pulse at 85 dB in the notodontid *Datana ministra*. Only the A1 cell responds to the sound; the non-auditory B cell (distinguished by the amplitude of its action potential) and motor neurones (two small action potentials following A1 firing) are not acoustically activated.

discharge rate and the percentage decrease in A1 discharge rate (Spearman rank correlation: r_S=–0.098, P=0.749, N=12).

We measured A1 cell adaptation (the change in the instantaneous firing rate) over the entire 45 ms duration of the stimulus pulse at 80 dB (the intensity that elicited the highest A1 firing rates) and 100 dB (that eliciting the greatest A1 drop-off). Fig. 3A shows that a specimen of *Datana ministra* with a high A1 drop-off (37 % from maximum) exhibits high adaptation compared with a specimen of *Schizura leptinoides* with low A1 drop-off (Fig. 3B). Fig. 3C compares the mean A1 firing rate of the *D. ministra* specimen in response to the first 10 ms of 100 dB stimulus pulses with that of their full

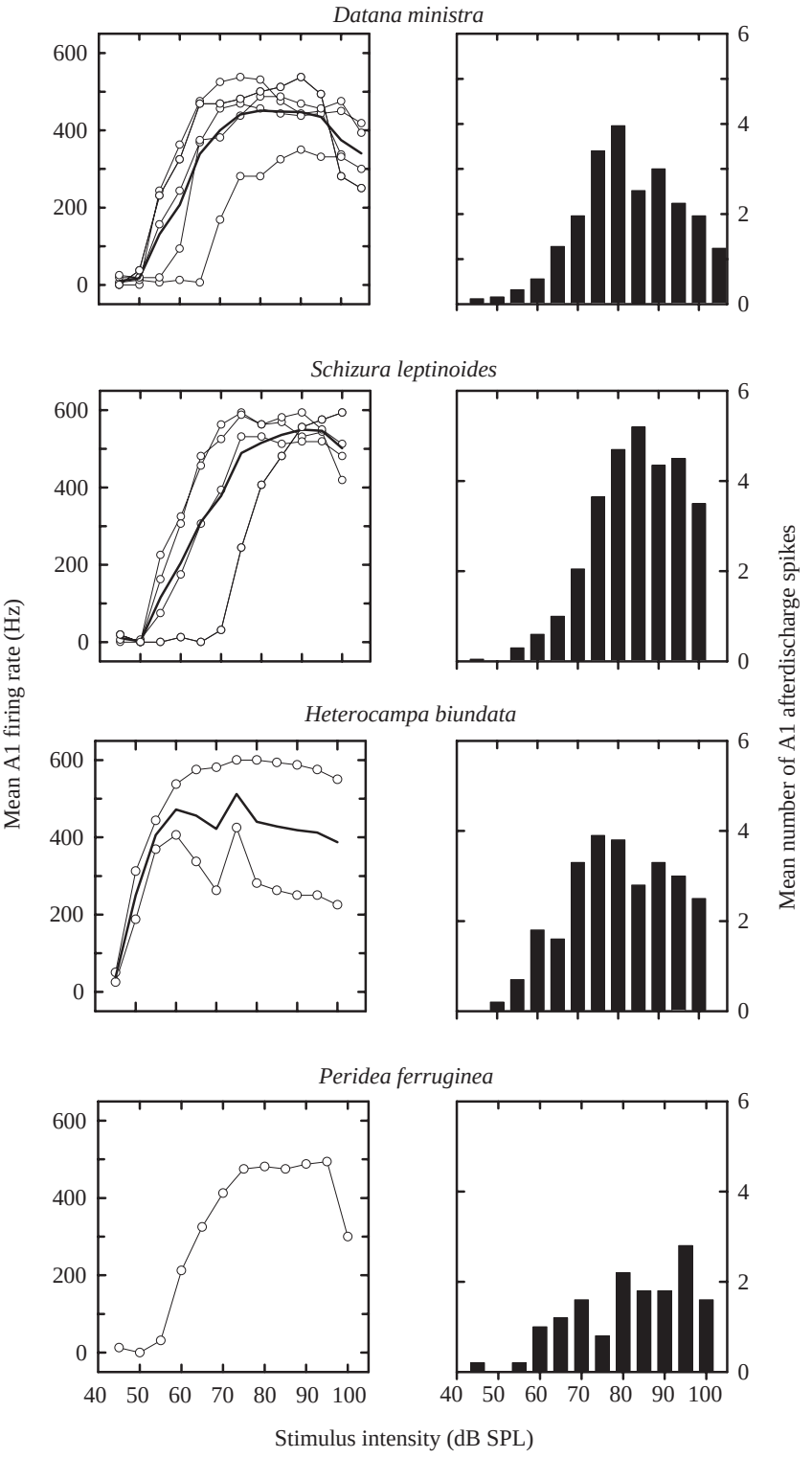

Fig. 2. The auditory response curves of the A1 cell in the notodontids *Datana ministra* (*N*=5), *Schizura leptinoides* (*N*=4), *Heterocampa biundata* (*N*=2) and *Peridea ferruginea* (*N*=1). The left-hand panel shows the mean firing rates of the A1 receptor in response to a 45 ms stimulus pulse at the different intensities used; open circles represent individual values, the solid line represents the mean of all specimens. In the right-hand panel, bar histograms are averaged A1 afterdischarge spike counts in response to stimulus pulses of different intensities.

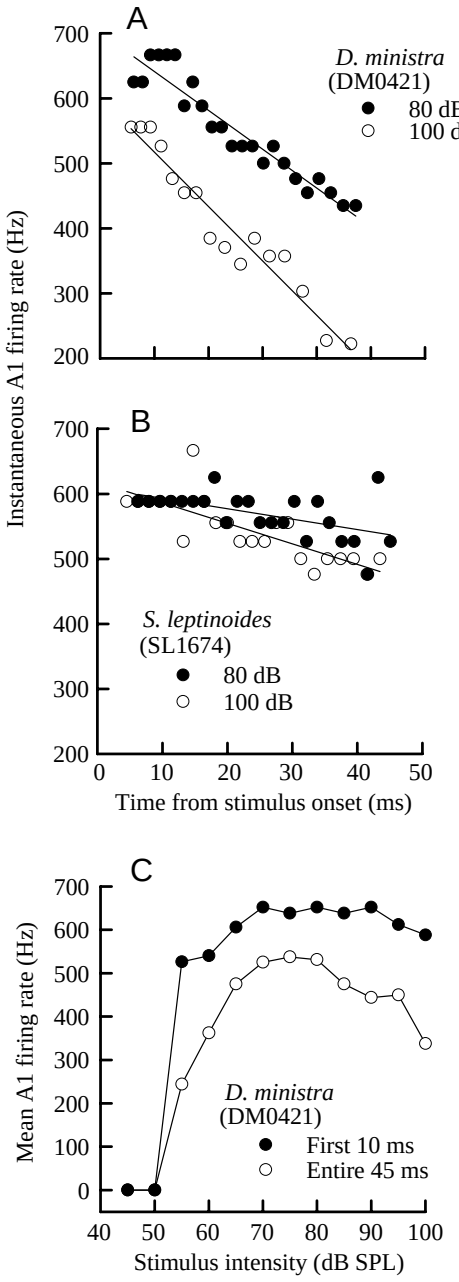

Fig. 3. A1 cell adaptation in specimens of *Datana ministra* (A) and *Schizura leptinoides* (B) that exhibited high and low levels, respectively, of A1 firing drop-off. Instantaneous A1 firing rates were remeasured in single-exposure trials to 45 ms stimulus pulses of 80 and 100 dB; regression lines (all significant at $P<0.05$) are drawn through the individual points at each stimulus intensity [DM0421: (80 dB) $F=213.7$, d.f.=21, $P<0.001$; (100 dB) $F=217.7$, d.f.=15, $P<0.001$; SL1674: (80 dB) $F=8.9$, d.f.=21, $P=0.007$; (100 dB) $F=35.5$, d.f.=20, $P<0.001$]. (C) Comparison of A1 firing rates in response to the full 45 ms and the first 10 ms of the stimulus pulses in the *D. ministra* specimen in A.

45 ms duration and demonstrates that A1 drop-off is more evident in response to longer stimulus pulses as a result of its greater adaptation (i.e. fewer total spikes) at these intensities.

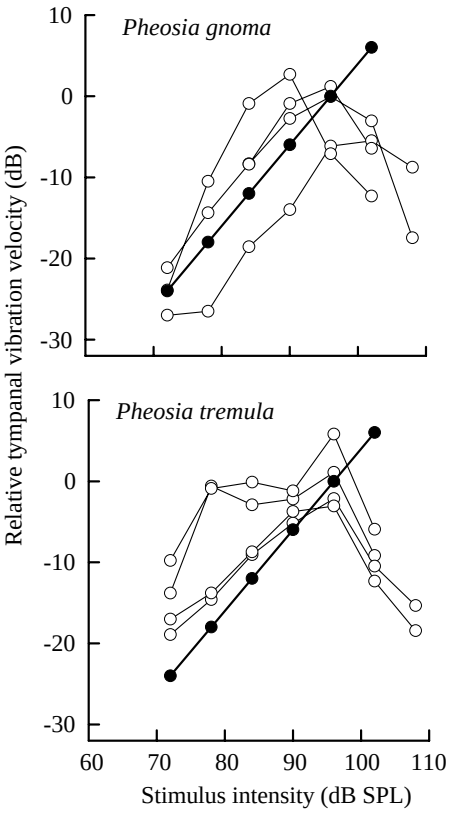

Fig. 4. Relative tympanal vibration velocities at 45 kHz of the Danish notodontids *Pheosia gnoma* and *Ph. tremula* determined using laser vibrometry. The heavy line shows the predicted increase in the expected vibration velocity assuming a linear tympanal motion over the whole stimulus range. In all specimens, linearity broke down at stimulus intensities above 90–96 dB SPL.

Tympanal vibration

Fig. 4 shows how the vibration velocity at 45 kHz varied with stimulus intensity in the Danish notodontids, *Pheosia tremula* and *Pheosia gnoma*. Every specimen tested showed an increase in vibration velocity that was qualitatively linear with stimulus intensity up to 90–96 dB SPL. At higher stimulus intensities, all specimens exhibited a reduction in vibration velocity from the maximum observed to that at the highest stimulus intensity tested, ranging from 5.9 to 18 dB with a mean drop of 11.7 dB. Using the reference vibration velocity of 6.3 mm s^{-1}, at 45 kHz the maximum vibration velocity measured [+5.8 dB for *Ph. tremula* (specimen 2) at 96 dB stimulus intensity] corresponds to a vibration amplitude of 22 nm.

Discussion

Our results demonstrate that the one-celled ears of some notodontids exhibit non-monotonic response curves similar to those reported for the two-celled ears of an arctiid moth, thus challenging the peripheral neural interaction hypothesis of Coro and Pérez (1983). The lack of correlation between

changes in the firing frequency of the B cell, the only other cell associated with the A cell (Surlykke, 1984), to increased stimulus intensities further removes any cellular influence on the A1 cell that could explain its reduction in discharge frequency. In the absence of an extraneuronal cause for the high-intensity A1 drop-off, the alternative explanations offered by Coro and Pérez (1983) need to be re-examined.

Receptor adaptation

The notodontid A1 cell adapts strongly at stimulus intensities that elicit drop-off, suggesting an intrinsic cellular cause. Adaptation results in reduced mean A1 firing rates only when measured over the entire 45 ms of stimulus but not over the first 10 ms (Fig. 3C), suggesting that stimulus length exaggerates the phenomenon of A1 drop-off. In specimens with a high A1 drop-off, this receptor initially fires at similar rates in response to stimulus intensities above those eliciting its maximal response (i.e. >80 dB), but it adapts more rapidly. Coro and Perez (1983) initially rejected receptor fatigue as an explanation for A1 drop-off in the arctiid *Empyreuma pugione* because of a strong poststimulus discharge in this receptor, although later results (Pérez and Coro, 1986*b*) indicated that this receptor characteristic is variable amongst species. In a recent paper, Coro *et al.* (1998) demonstrate that the number of A1 spikes per stimulus pulse does not decrease at stimulus repetition rates of 2 Hz, further suggesting that fatigue, in the strict sense, is not occurring in the A1 cell. Adaptation could, however, still occur within the duration of each stimulus pulse, resulting in a lower mean firing rate per pulse at high intensities. All the notodontids we tested exhibited postexcitatory A1 cell suppression in response to high-intensity stimuli, even in those specimens without A1 drop-off (e.g. *S. leptinoides*, SL1674), suggesting that it is not high firing rate *per se* that leads to adaptation, but rather the initial transduction process from mechanical stimulus to generator potential.

In mammalian auditory systems, non-monotonic rate-level curves are characteristically found in higher-order neurones (Rhode and Greenberg, 1992), whereas the primary fibres in the auditory nerve show saturating rate-level curves (Ruggero, 1992). However, it was recently reported that a small proportion of the auditory fibres in the frog *Rana temporaria* also show non-monotonic rate-level curves (Christensen-Dalsgaard *et al.* 1998). In this frog, as in our moths, the drop-off seems to be correlated with the response becoming more phasic (i.e. adapting more rapidly) with increasing stimulus intensity, suggesting a common physiological mechanism in these two phylogenetically distant ears.

Tympanal motion non-linearity

Our vibrometry results provide evidence that the tympanal vibrations of two species of notodontids do not increase linearly with stimulus intensity, suggesting that A1 drop-off is partly caused by reduced tympanal vibration amplitudes at high stimulus intensities. Coro and Pérez (1983, 1984) and Pérez and Coro (1986*b*) originally rejected this explanation because the noctuoid A2 cell is attached near to the same place on the tympanic membrane as the A1 cell (Ghiradella, 1971) and yet does not undergo discharge reductions at high intensities. We have no satisfactory explanation for this observation in the light of our tympanal motion results other than the possibility that the lower overall firing rate of the A2 cell suggests a mechanical coupling between the tympanum and the dendrite of this cell that is less affected by a reduction in the amplitude of tympanal movements.

At first glance, the non-linearity of the ear of notodontids at high sound intensities is not in keeping with other insect tympana. Paton *et al.* (1977) demonstrated tympanal linearity in another naked tympanum, that of the cricket *Gryllus pennsylvanicus*, at stimulus intensities up to approximately 110 dB SPL, Schiolten *et al.* (1981) suggested that tympanal movements in the noctuid moth *Agrotis segetum* are linear at 100 dB (although they did not relate tympanal motion to varying stimulus intensities) and Breckow and Sippel (1985), using stroboscopic methods, showed tympanal linearity for the locust *Locusta migratoria* from 90 to 110 dB SPL (a species previously demonstrated to possess non-monotonic auditory responses; Sippel and Breckow, 1984). Kössl and Boyan (1998), however, have recently suggested that otoacoustic emissions from the stimulated tympana of *L. migratoria* arise from non-linearity at low intensities, and these results combined with ours suggest that non-linear phenomena in insect ears may be more common than previously assumed.

We conclude that the non-monotonic firing response of the A1 receptor in notodontid moths is caused by a combination of tympanal non-linearity and cellular adaptation brought about from long stimulus durations. We also conclude that the close phylogenetic relationships between notodontids and noctuids, in combination with the anatomical absence of cellular connections, makes it unlikely that the A2 cell in noctuids causes A1 drop-off as proposed by Coro and Pérez (1983, 1984).

What is the biological relevance of the A1 response curves in these moths? Aerially hawking bats (e.g. *Eptesicus fuscus*; Kick and Simmons, 1982) emit echolocation intensities of 90–100 dB, values higher than those where the A1 cell begins its drop-off in both one- and two-celled noctuoids. These intensities, however, would not be reached until the bat was 10–50 cm away from the moth and, assuming that the moth has been aware of the bat's approach since it was first detected 30–40 m away (Roeder, 1967), changes in the firing responses of the A1 cell may not affect whatever postsynaptic activity has already been elicited. Fullard (1987) and Boyan and Fullard (1988) suggest that, once a critical A1 firing rate above spontaneous level is achieved, the moth's central nervous system is alerted from a 'no-bat' to a 'bat' condition so that, once evasive flight responses (e.g. flight cessation) are activated, a reduction in A1 firing frequency at higher intensities might not affect the moth's responses.

Although providing insights into basic auditory mechanisms, the results of our studies and earlier studies warn against the use of biologically unusual stimuli when testing for

evolved sensory adaptations. Assuming that bat detection is the only function of the majority of moth ears (Fullard, 1998), it is to bat echolocation calls that these organs have evolved their response characteristics. Although some bats emit long (>10 ms) echolocation pulses (e.g. *Rhinolophus ferrumequinum*; Simmons *et al.* 1979), most use calls of 10 ms or shorter while aerially foraging. Since bats shorten their calls as they approach an intended prey, the combination of long stimulus durations and high intensities used in our experiments and earlier experiments can represent biologically unusual acoustic stimuli for most moths. Exceptions to this condition could exist in the rare cases of auditory responses of certain moths to long conspecific social signals (e.g. Sanderford *et al.* 1998), and the significance of the reduced A1 response at high intensities in these unique circumstances remains unknown.

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