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HEARING IN NOTODONTID MOTHS: A TYMPANIC ORGAN WITH A SINGLE AUDITORY NEURONE

By ANNEMARIE SURLYKKE
Institute of Biology, Odense University, DK-5230 Odense M, Denmark

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SUMMARY

1. Notodontid moths possess paired tympanic organs basically similar to the ears in other noctuoid families, but with a single auditory *A* cell. The *A* cell and the non-auditory *B* cell were studied anatomically by infusion of $CoCl_2$ and physiologically by recordings from the tympanic nerve.

2. The response of the *A* cell is determined by intensity parameters and temporal parameters of an ultrasonic stimulus. The notodontid ear is as sensitive as the ears of sympatric noctuids. The directional sensitivity is approximately the same as in noctuids of comparable size (maximal interaural intensity difference of 10–15 dB). The dynamic range of the *A* cell is about 20–25 dB. Sound levels exceeding the threshold by 30–40 dB will saturate the *A* cells in both ears. Stimuli with different pulse lengths (from 5 to 200 ms, corresponding to pulse repetition rates (PRR) from 100–2·5 Hz), but equal duty cycles (50 %) gave a maximum response for pulse lengths lying between 30 and 50 ms. The receptor cell followed the sound pulses in a one-to-one manner even at a PRR of 200 Hz.

3. Notodontid moths seem to show the same 'bimodal' evasive behaviour as noctuids. This behaviour can be explained on the basis of intensity parameters, since only low intensity stimuli will give the notodontid directional information. Hence, directional evasive behaviour is expected at low sound pressure levels (SPL), while high SPL (saturating both *A* cells) should elicit a non-directional evasive behaviour. However, the evasive behaviour could also be explained in terms of time parameters. Hunting bats increase the PRR of their cries when closing in on a prey and the moths may be able to use these time cues for changing their behaviour.

INTRODUCTION

Moths of the superfamily Noctuoidea possess paired tympanic organs, located in recesses on the metathorax, which appear to serve a single purpose: detection of the ultrasonic cries of bats. The moths investigated so far (mainly Noctuidae) show a 'bimodal' response to ultrasound. They either fly directly away from the sound source or commence a series of complex manoeuvres (Roeder, 1962, 1974; Agee, 1969).

Three sensory cells are found in the ear of noctuid moths, two *A* cells that are sensitive to ultrasound and a non-auditory *B* cell (Treat & Roeder, 1959; Lechtenberg, 1971). The two *A* cells are contained in a scoloparium, which is attached directly

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to the tympanic membrane (Eggers, 1919; Ghiradella, 1971). Physiological studies have revealed parallel frequency response curves for the two cells (Suga, 1961; Surlykke & Miller, 1982), but a difference of 20 dB in sensitivity is found between A_1, the more sensitive cell, and A_2 (Roeder, 1974).

Roeder (1974) pointed out that the type of information reaching the central nervous system (CNS) will depend on whether one or both *A* cells are excited. He suggested that the change in sensory information might coincide with the behavioural transition from the steered turning-away (negative phonotaxis), which is seen at low sound pressure levels (SPL), to the apparently random, complex manoeuvres associated with high SPLs. This suggestion means, in essence, that activity in just a single cell, A_2, triggers a shift from one behaviour to another depending on the SPL. However, the suggestion is still speculative. Field studies have not revealed the distance (and consequently sound intensity) at which the behavioural change occurs or whether there is some transitional form of behaviour. Also, determining the effect on behaviour of each cell separately at high sound intensities has not been possible, since both *A* cells are excited at an SPL exceeding the threshold of A_2. The ears of one noctuoid family, the Notodontidae, are basically similar to those of Noctuidae, but contain only a single auditory sensory cell (Eggers, 1919). Roeder anticipated that Notodontidae would show a monomodal behaviour.

The purpose of this study was to confirm the presence of a single *A* cell in the notodontid ear, and to obtain physiological evidence regarding the amount of information transmitted to the CNS by this simple ear. The control of evasive behaviour in tympanate moths is discussed on the basis of the results. Some of the results have been reported briefly (see Miller, 1982, 1983).

MATERIALS AND METHODS

Animals

Notodontid moths of the species *Pheosia tremula, Phalera bucephala* and a few *Pterostoma palpina* were captured in a light trap in the vicinity of Odense University, Denmark. Laboratory-reared *Phalera bucephala* individuals were also used for physiological and anatomical investigations. The noctuids used for comparison were *Agrotis segetum* (kindly provided by the Institute of Plant Protection, Lyngby, Denmark) and *Barathra brassicae* (laboratory-reared from eggs and pupae kindly donated by Dr H. Bathon, Institut für biologische Schädlingsbekämpfung, Darmstadt, F.R.G.).

Anatomy

Backfilling with cobalt chloride and subsequent intensification by Timm's method was used to trace the central axons of the sensory cells in the ear of the notodontids, as described previously (Surlykke & Miller, 1982). Backfillings were done on 19 *Pheosia tremula*, three *Phalera bucephala* and two *Pterostoma palpina*. Fourteen of the *Pheosia tremula*, two of the *Phalera bucephala* and one of the *Pterostoma palpina* (a total of 17 successful preparations) showed profiles of one or two central sensory axons. None showed more than two axons. (These preparations showed a maximum

shrinkage of 30 % in length.) $CoCl_2$ fillings of the peripheral part of the sensory cells were done in essentially the same way: by letting $CoCl_2$ diffuse distally through the tympanic nerve, III N1b, which was cut close to the connection with III N1. After 4 to 20 h at room temperature the cobalt was precipitated and the tissue fixed in alcoholic Bouin. The ear was isolated and intensified. Ten *Phalera bucephala* and five *B. brassicae* were treated in this way. The descriptions given here are based on five successful preparations of *Phalera bucephala* and two of *B. brassicae*.

Electrophysiology

The tympanic nerve was exposed by a modification of the technique described by Roeder (1966*a*, 1974), and attached to an extracellular tungsten hook electrode. The action potentials were recorded using conventional electrophysiological techniques. The moth was mounted 30 cm away from an electrostatic loudspeaker with one ear facing the sound source. The diameter of the loudspeaker was 60 mm, so a distance of 30 cm means that the moth was in the farfield when using ultrasound. Acoustic stimuli were delivered to the moth as continuous trains of pulses with carrier frequencies ranging from 10 to 100 kHz. 5-ms pulses with a rise/fall time of 0·5 ms and with a pulse repetition rate (PRR) of 5 Hz were used for threshold determinations and directionality studies. Stimuli with different PRR and pulse durations were used for studying temporal responses. The stimuli were generated using a Wavetek oscillator (model 112) triggered by a Grass SD9 Stimulator, sent through a Brüel & Kjær 1/3 octave band pass filter Type 1614. (Energies of harmonics were negligible at frequencies of 25 kHz or higher. Echoes were attenuated by at least 20 dB.) Sound pressure levels (SPL) are given in dB (re 20 μPa).

RESULTS

Structure

Infusion of $CoCl_2$ distally revealed a single *A* cell and a *B* cell in the ear of *Phalera bucephala* (Fig. 1A). The ovoid soma of the *A* cell was located about 30 μm from the tympanum. The axon was 2–3 μm wide. The *B* cell resembled *B* cells found in noctuid moths, but lay on the wall of the tympanic cavity, since no Bügel was found in the notodontids studied. The axon of the *B* cell, which was 4–5 μm wide, joined that of the *A* cell at a point about 150 μm proximal to the soma of the *A* cell. Similar fillings in a noctuid moth (*B. brassicae*) were done for comparison. These clearly showed the profiles of two cells in the scoloparium, and a *B* cell on the Bügel (Fig. 1B). The notodontid ear also differed from that of other noctuoid moths by having no abdominal hood covering the tympanic recess and no nodular sclerite, making the conjunctiva continuous with the tympanum.

Backfillings with $CoCl_2$ through the tympanic nerve were done mostly on *Pheosia tremula*. Backfilling revealed the profiles of two sensory axons with basically similar branching patterns (Fig. 2). The afferent axons ran close together in III N1, and they remained ipsilateral to III N1b after entering the metathoracic ganglion. (In contrast to other noctuoid families the notodontids had short but distinct connectives between the meso- and metathoracic ganglion allowing for a clear distinction between these

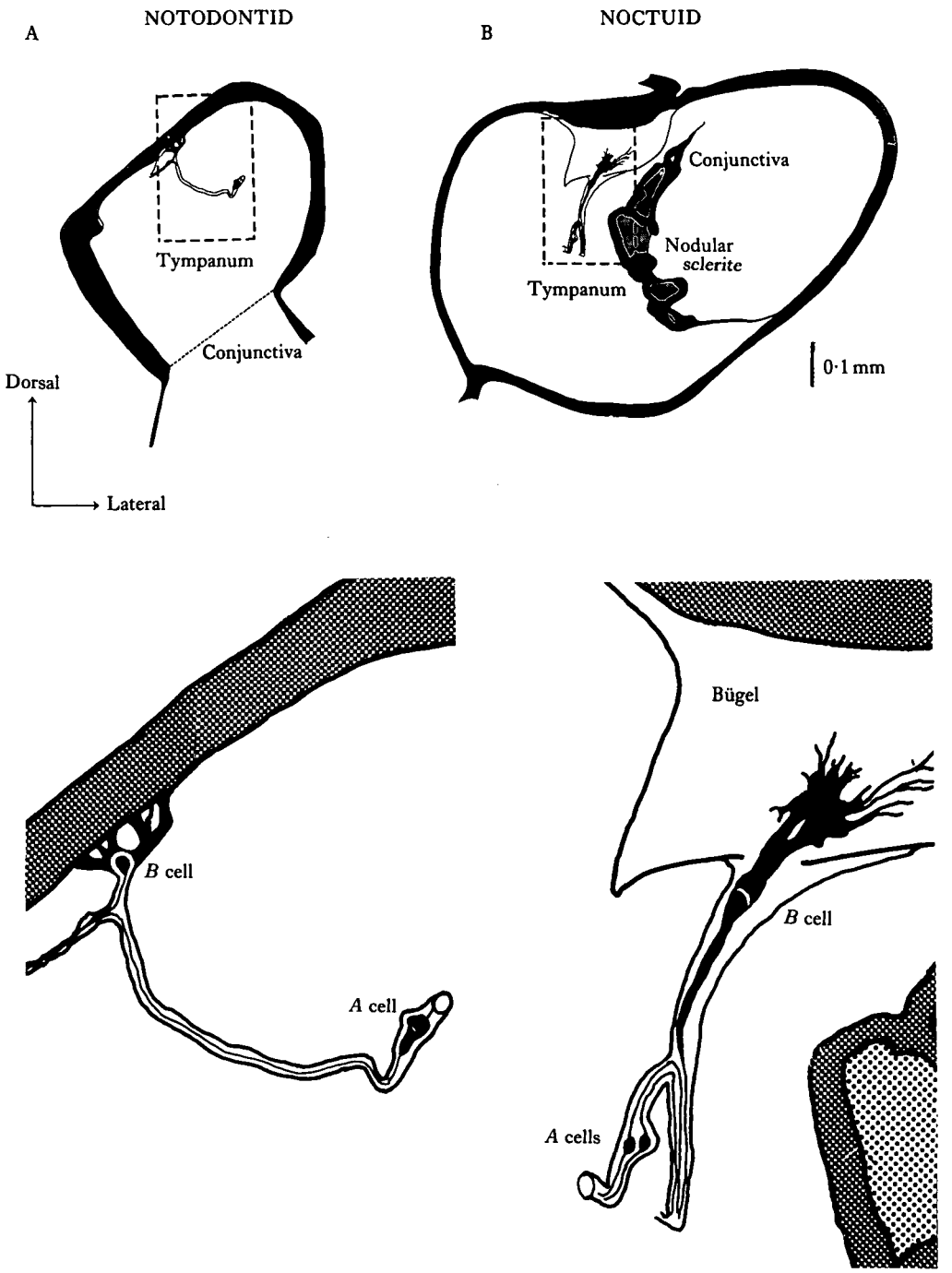

Fig. 1. *Camera lucida* drawings of the $CoCl_2$-stained sensory cells in the right ear of a notodontid *Phalera bucephala* (A) and a noctuid *Barathra brassicae* (B). In the notodontid a single *A* cell is contained in the scoloparium, which is attached to the centre of the tympanum. No Bügel is found in notodontids, so the *B* cell is attached to the sclerotized ring surrounding the tympanum (A). In the noctuid two *A* cells are seen in the scoloparium and the *B* cell is attached to the Bügel (B).

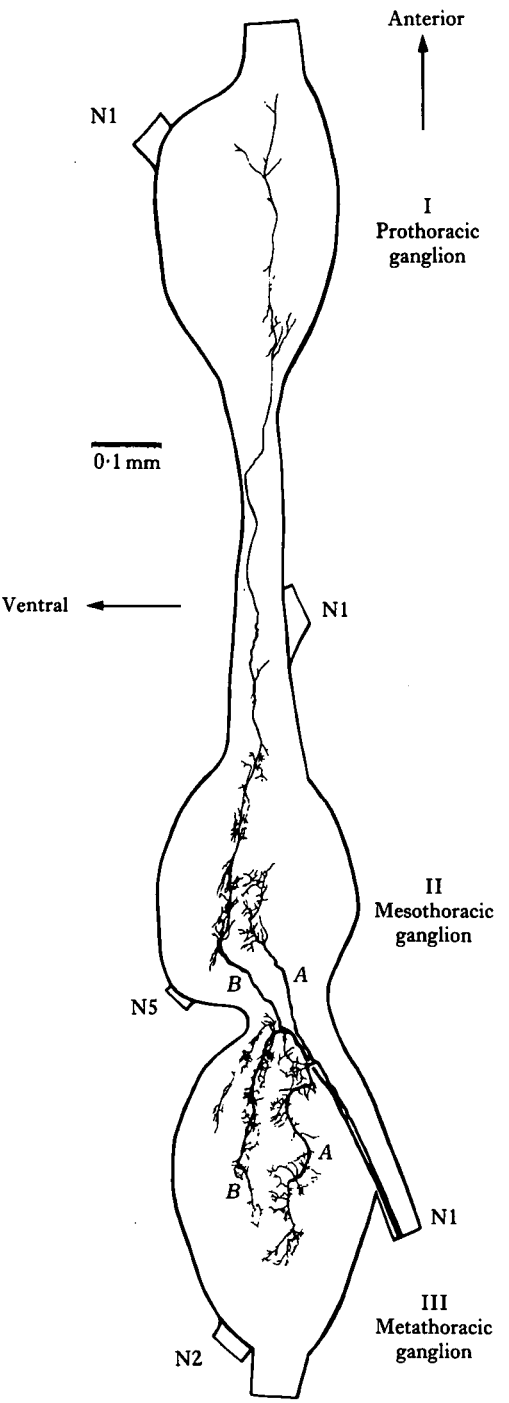

Fig. 2. Central branchings of the two sensory cells of *Pheosia tremula* (Notodontidae). The *camera lucida* drawing shows the prothoracic, mesothoracic and metathoracic ganglia from the right side. The branchings of the auditory *A* cell and the non-auditory *B* cell remain ipsilateral.

ganglia.) Both axons divided into an anterior and a posterior branch. The most lateral and dorsal axon was assumed to be that of the *A* cell while the medial ventral one was the central projection of the *B* cell (see Discussion). The anterior and posterior branches of the *A* cell were 1–2 μm in diameter. The posterior branch terminated in the posterior half of the metathoracic ganglion and gave off numerous side branches. Some of the posterior side branches appeared to intermingle with those of the *B* cell. The anterior branch terminated in the central portion of the mesothoracic ganglion. The *A* cell stained in 12 of the 17 successful preparations. Both branches of the *B* cell also had diameters of 1–2 μm. The posterior branch extended as far back in the metathoracic ganglion as that of the *A* cell. It had several short side branches. The anterior part of the *B* cell had branches ending in the prothoracic ganglion as well as branches extending into the cervical connectives. The *B* cell stained in 16 of the 17 good preparations. As in noctuids, some preparations showed the profiles of five motoneurones in the mesothoracic ganglion (Surlykke & Miller, 1982). The cell body and branches of one lay contralateral to III N1b. The four others lay ipsilateral and close together. They branched profusely in the same region as the anterior branch of the *A* cell. The central branchings of *A* and *B* from the two other notodontids studied (*Phalera bucephala* and *Pterostoma palpina*) closely resembled those of *Pheosia tremula*.

Physiology

The electrophysiological recordings from nerve III N1b confirmed the anatomical findings. The recordings from *Pheosia tremula* showed spikes from two cells, one that was not affected by the sound stimulus (the *B* cell) and one whose activity was correlated with the ultrasonic stimulus (the *A* cell). Spikes from more than one *A* cell were never seen, irrespective of the SPL (Fig. 3A). Similar experiments with noctuids clearly showed the spikes of two *A* cells at high sound intensities (Fig. 3B).

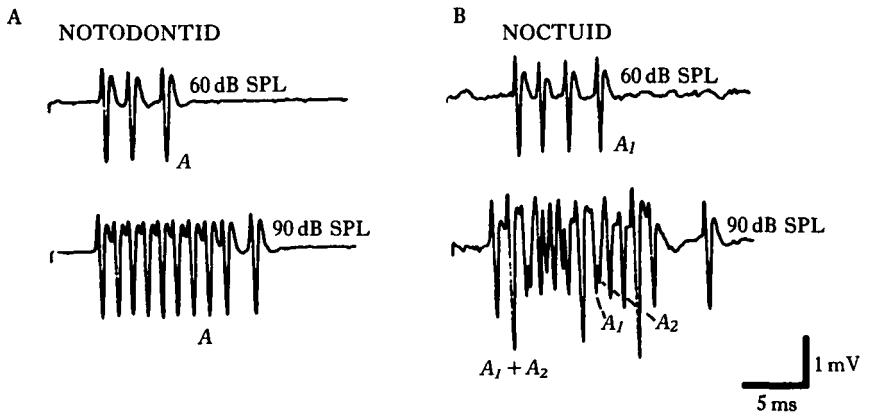

Fig. 3. Recordings from the tympanic nerve of a notodontid *Pheosia tremula* (A) and a noctuid *Agrotis segetum* (B). In the notodontid only one cell responds to ultrasound irrespective of sound pressure level (A). The A_1 cell is excited at low sound intensities in the noctuid, while both *A* cells fire at high sound intensities. The spikes are too close together to have originated from the same cell (B). No spikes from the *B* cells are seen in these recordings.

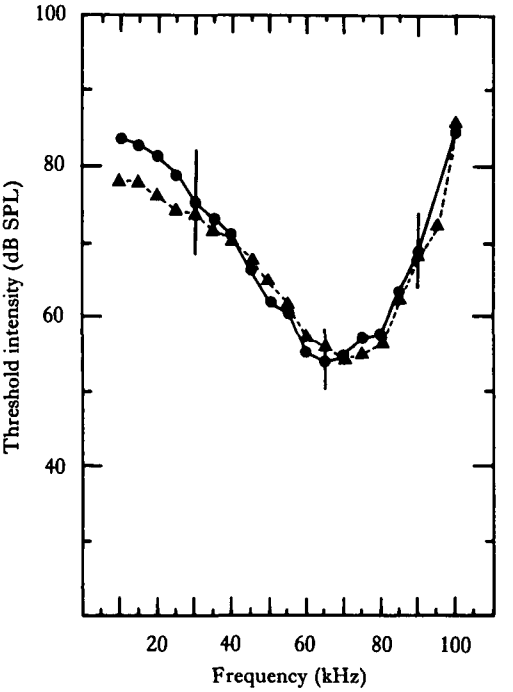

Fig. 4. Auditory threshold curves of the two notodontids *Pheosia tremula* (●) and *Phalera bucephala* (▲). The threshold and the tuning are similar for the two sympatric species. (Vertical bars represent 1 S.D., given here for *Pheosia tremula*. The S.D. values are representative for both species; $N = 10$ for both species.) Thresholds were found on wingless moths.

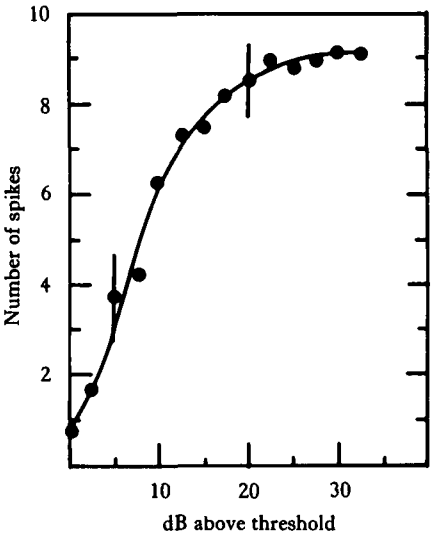

Fig. 5. Dynamic range of a notodontid moth ear (*Phalera bucephala*). The total number of spikes for a 5-ms sound pulse is shown as a function of the sound intensity with threshold at 40 kHz. (Vertical bars represent typical ±1 S.D., $N = 6$.)

The threshold was defined as the SPL necessary to elicit 1–2 spikes in at least 8 of 10 stimulations with 5-ms pulses. The spontaneous activity of the *A* cell was very low and did not interfere with threshold determinations. Both *Pheosia tremula* and *Phalera bucephala* were most sensitive in a range from 20 to 50 kHz (Fig. 4). At 45 kHz, which was the best frequency for *Pheosia tremula*, the threshold was 54·0 ± 4·1 dB (S.D., $N = 10$), while *Phalera bucephala* had a threshold of 54·2 ± 3·9 dB (S.D., $N = 10$) at its best frequency (40 kHz). The threshold determinations were done on wingless moths.

The dynamic range of the *A* cell was determined in three different ways: by the number of spikes elicited by one 5-ms pulse (Fig. 5), by the average spike rate in the response trains, and by the latency to the first spike for various sound pressures. All three methods gave dynamic ranges of about 20–25 dB for *Pheosia tremula* and *Phalera bucephala*.

The directional sensitivity of the notodontid moth ear was found by computing the threshold curve for the ipsilateral ear when sound impinged ipsilaterally, contralaterally and from ahead. Experiments were performed on wingless moths (Fig. 6A) as well as on winged moths, (*Pheosia tremula*, wingspan 18–28 mm). The wings were fixed in three different positions: horizontally, and at the highest and the lowest position assumed by the wings in free flight (Fig. 6B,C,D). The threshold difference between the ipsi- and contralateral ear reached a plateau at 40–50 kHz and had a value of 15–20 dB. The maximum average value was approximately the same irrespective of wing presence or position, but the wings did influence the directionality, since the variation was much greater for winged

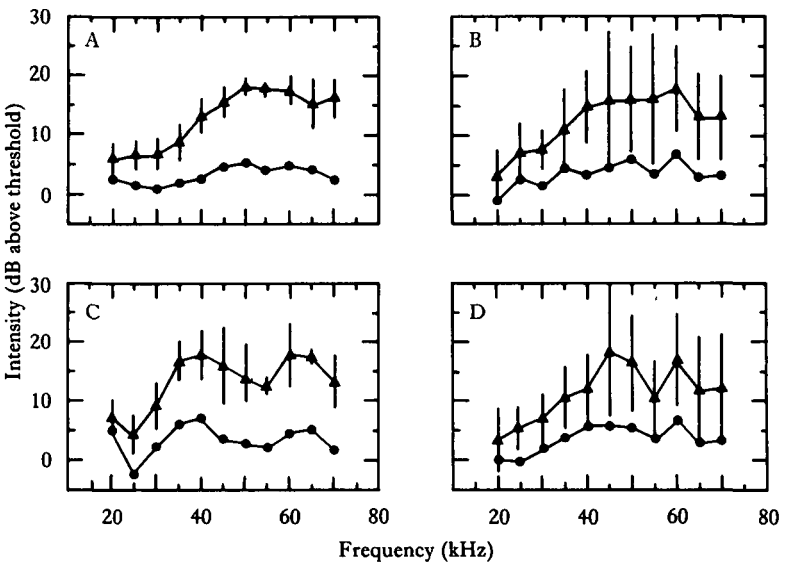

Fig. 6. Directional sensitivity of *Pheosia tremula* (Notodontidae). The audiograms for the ipsilateral ear are shown for sound coming from ahead (●) and from the contralateral side (▲). The sound intensities refer to the threshold for sound coming from the ipsilateral side. (A) shows the results from moths without wings, (B) from moths with wings horizontal, (C) from moths with the wings in the highest and (D) in the lowest position assumed in natural flight. (Vertical bars represent ±1 S.D., $N = 5$.)

preparations. This larger variation probably reflects the fact that small differences in the exact alignment of the moth with respect to the sound source are more important for winged preparations because of the acoustic 'shadow' from the wings. At the end of each experiment the sensitivity was rechecked with sound from the ipsilateral side. The results were not included in the analysis if the sensitivity had changed more than 4 dB.

Both behavioural and electrophysiological results indicate that time parameters of the sound stimulus might be important to the moth (see Discussion). The auditory sensory cells of *Pheosia tremula* were able to follow PRRs as high as the highest repetition rates in bat cries. At threshold for a 3-ms pulse, the *A* cell could follow a PRR of 50 Hz, but a PRR of 200 Hz could be followed at SPLs exceeding the threshold by at least +10 dB. The importance of time parameters was also investigated by stimulating with two types of continuous pulse trains with equal duty cycle (50 %). One type had 50 ms pulse and pause lengths giving a PRR of 10 Hz. The other type had 5 ms pulse and pause lengths giving a PRR of 100 Hz. The total number of spikes during the first second of stimulation was recorded at sound intensities ranging from threshold up to +35 dB of threshold (e.g. Fig. 7). PRRs of 10 Hz and 100 Hz gave approximately the same number of spikes when stimulating with sound intensities just above threshold, but at SPLs from about +15 dB of threshold a significantly greater number of spikes was seen for a 10 Hz stimulus than for a 100 Hz stimulus. At +20 dB of threshold a PRR of 100 Hz elicited 130 ± 24 spikes (S.D., $N = 5$) during the first second of stimulation while 10 Hz elicited 173 ± 24 spikes (S.D., $N = 5$). The difference in number of spikes is statistically significant ($P < 0{\cdot}01$, paired Student's *t*-test). Responses to PRR from 2·5–100 Hz (still with duty cycles of 50 %) were recorded at +15 dB of threshold. The results suggest that optimal stimuli had pulse lengths between 30 and 50 ms giving PRRs from 16·7–10 Hz (Fig. 8).

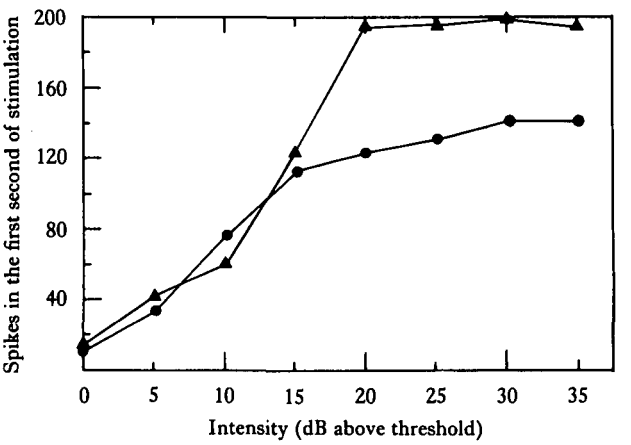

Fig. 7. Number of spikes from the *A* cell in *Pheosia tremula* (Notodontidae) during the first second of stimulation. The lower curve (●) shows the response to a train with pulse lengths/interpulse lengths of 5 ms (100 Hz), while the upper curve (▲) shows the results for a train with pulse lengths/interpulse lengths of 50 ms (10 Hz). (Duty cycle = 50 %.) The dB values refer to threshold for a single 5-ms pulse. Although the sound intensity and the duty cycle are the same, significantly more spikes are seen when stimulating with 10 Hz than with 100 Hz. The curves are from a single typical individual.

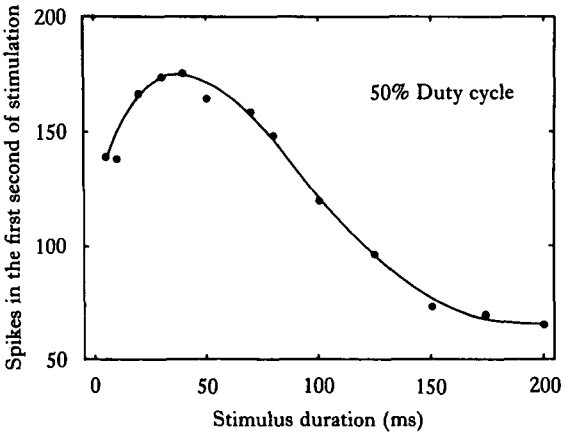

Fig. 8. Number of spikes from the *A* cell in *Pheosia tremula* (Notodontidae) elicited by stimulus trains with the same duty cycles (50 %) but different pulse lengths at 15 dB above threshold. The most effective stimuli have 30–50 ms pulse lengths corresponding to PRRs from 17 to 10 Hz. Results from a single individual.

DISCUSSION

Notodontidae possess the simplest known ear with just one auditory *A* cell. $CoCl_2$ staining never showed profiles of more than two sensory cells. This corresponds with the recordings from the tympanic nerve, where spikes from only two cells, one *B* cell and one *A* cell, were seen.

The two axons filled through III N1b are likely to be those of the two sensory cells in the ear. Firstly, the basic branching patterns resembled closely the branching patterns of the three sensory axons from the ear of noctuid moths (Surlykke & Miller, 1982; Paul, 1973). Secondly, backfilling through III N1b never revealed more than two sensory axons lacking central cell bodies. This corresponded to the number of sensory cells showing spikes when recording from the tympanic nerve, and to the number of cells filled by distal infusion of $CoCl_2$ through III N1b. The cells can only be identified on the basis of homology. In Noctuidae the *B* cell extends through all three thoracic ganglia. In Notodontidae only the medial ventral axon branches in all three ganglia and is likely to be the *B* cell. Accordingly the dorsal lateral axon must be that of the *A* cell, which seems to be homologous to the A_2 cell of noctuids.

The directional sensitivity of *Pheosia tremula* was similar to that of noctuids of comparable size: 7–12 dB for *Caenurgina erechtea* and 15–20 dB for *Heliothis zea* (Roeder, 1966*b*). Payne, Roeder & Wallman (1966) found a 20–40 dB maximum difference in sensitivity between the ipsi- and contralateral ear of red underwing moths with wing spans between 60 and 95 mm. The results of mechanical recordings from the tympanic organ of noctuid moths could be interpreted as an indication that the moth ear is a pure pressure receiver (Schiolten, Larsen & Michelsen, 1981; Michelsen, 1983). However, the two ears are connected by internal air sacs, so theoretically the moth ear could be a pressure gradient receiver. If the moth ear were a pressure receiver, the directional sensitivity would be due to diffraction. The theoretical curve for diffraction around a body as complex as a moth is not known and even

models for simpler geometrical forms are very complicated. If the moth without wings is regarded as a cylinder with a radius of 4 mm (Fig. 6A), a surplus pressure should start building up at around 13 kHz and around 60–70 kHz the difference between the side facing the sound source and the side facing away from the sound source should reach a plateau of 12–16 dB (Skudrzyk, 1971). This is in agreement with the results. Fig. 6 also shows that when the wings are up, the plateau is reached at a lower frequency. This is as expected, because the upward position of the wings gives the body the largest diameter, thereby increasing radius compared to wavelength (compare Fig. 6A and 6C). Presumably acoustic directionality is similar in moths of similar size irrespective of the anatomy of the ear. This indicates that the pattern of acoustic directionality found for the red underwing moths (Payne *et al.* 1966) is also valid for the Notodontidae when corrected for size.

Some inconsistency exists in the literature regarding the dynamic range of the *A* cells in Noctuidae. Values from 20 to 40 dB have been reported (Suga, 1961; Roeder, 1966*a*; Adams, 1971). The discrepancies are probably due to difficulties in distinguishing between A_1 and A_2 spikes. This problem does not exist in the Notodontidae and here the dynamic range is 20–25 dB. The homology between the *A* cells in Notodontidae and Noctuidae indicates that the dynamic range of each *A* cell in Noctuidae is about 20 dB, in agreement with Roeder's results (Roeder, 1966*a*).

The control of the bimodal evasive behaviour shown by noctuids has been ascribed to the combined activity of A_1 and A_2 depending on intensity (Roeder, 1974). However, the present results prompt a reconsideration of the role of the two *A* cells since a similar bimodal evasive behaviour would be expected for notodontids on basis of the sensitivity, directionality and dynamic range of their *A* cell. The peak sensitivity of the *A* cell is approximately equal to that of the A_1 cell of the sympatric noctuid, *Agrotis segetum* (Surlykke & Miller, 1982), and it corresponds well with values from other noctuids (Agee, 1967; Fenton & Fullard, 1979). Hence, notodontids and noctuids can detect approaching bats equally well. At a moderate SPL, where neither of the *A* cells in the two ears is saturated, the notodontid will get information about distance and direction to the sound source. The expected evasive behaviour would be a negative phonotaxis. At SPL exceeding the threshold by 30–35 dB the *A* cells of both ears will be saturated. In this case neither distance nor direction to the sound source can be detected and an evasive behaviour without directional elements would be expected. Preliminary behavioural experiments confirmed these expectations. Notodontids flying in a large cage, and notodontids attracted to a light trap in the field, were 'shot' with ultrasonic pulses from an electrostatic loudspeaker mounted on a rifle stock. The moths clearly showed negative phonotaxis as well as loops and dives to the ground. However, accurate measurements of the distance to the moths were not possible, so the SPL at the moth's ear could not be calculated. More experiments with notodontid behaviour under carefully controlled conditions are clearly needed.

Alternatively, the behaviour could be explained on the basis of temporal changes in the stimulus. Previous results for noctuids indicate that time parameters might be important. Only stimuli within a certain range of PRRs will result in constant behavioural responses (Roeder, 1962, 1967) and most of the interneurones found so far in the moth CNS integrate time parameters (reflected by their descriptions i.e. repeaters, pulse markers and train markers) (Roeder, 1966*b*). The *A* cell of *Pheosia*

tremula responded maximally to stimuli with PRR between 10 and 17 Hz, probably reflecting the time course of excitation and adaptation. Hence, the response of the primary sensory cell is influenced by the temporal pattern of the stimulation (Figs 7, 8). Time parameters might be good clues for tympanate moths since all known insectivorous bats, which catch their prey on-the-wing, have the same pattern of hunting cries: in the search phase the cries are rather long (5–100 ms) and repeated slowly (5–10 Hz). Cries of the approach phase, which starts when the bat first reacts to a possible target, become shorter and the PRR progressively increases. In the terminal phase, when the bat closes in for the capture (around 0·5 m from the prey), the cries can be as short as 0·5 ms and repeated at PRRs of up to 100–200 Hz (Simmons, Fenton & O'Farrel, 1979). Consequently, by means of the PRR the bat codes how far it believes itself to be from a potential target. The ear of a notodontid moth can follow a PRR of up to 50 Hz at threshold, but at sound intensities over +15 dB of threshold (around 70 dB SPL) the ear can follow cry rates of up to 200 Hz. Many bats cry with intensities around 110 dB SPL measured 10 cm in front of the bat's mouth, corresponding to about 96 dB SPL at 0·5 m. This means that the SPL at the moth's ear in the terminal phase should be high enough to enable the *A* cell to follow the high cry repetition rate. Hence, notodontid moths can theoretically compensate for the lesser dynamic range compared to noctuids, by using time clues for distance detection at close range. (Noctuids are of course not excluded from using temporal parameters. *B. brassicae* can follow PRR of 200 Hz, B. M. Madsen, personal communication.) Future experiments will probably show that the moths use both sources of information for 'decision making'.

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