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Otoacoustic emissions from insect ears having just one auditory neuron

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Abstract Sensitive hearing organs often employ nonlinear mechanical sound processing which produces distortion-product otoacoustic emissions. Such emissions are also recorded from insect tympanal organs. Here we report high frequency distortion-product emissions, evoked by stimulus frequencies up to 95 kHz, from the tympanal organ of a notodontid moth, *Ptilodon cucullina*, which contains only a single auditory receptor neuron. The 2*f*1–*f*2 distortion-product emission reaches sound levels above 40 dB SPL. Most emission growth functions show a prominent notch of 20 dB depth ($n = 20$ trials), accompanied by an average phase shift of 119°, at stimulus levels between 60 and 70 dB SPL, which separates a low- and a high-level component. The emissions are vulnerable to topical application of ethyl ether which shifts growth functions by about 20 dB towards higher stimulus levels. For the mammalian cochlea, Lukashkin and colleagues have proposed that distinct level-dependent components of nonlinear amplification do not necessarily require interaction of several cellular sources but could be due to a single nonlinear source. In notodontids, such a physiologically vulnerable source could be the single receptor cell. Potential contributions from accessory cells to the nonlinear properties of the scolopidial hearing organ are still unclear.

Keywords Distortion-product otoacoustic emissions · DPOAE · Notodontid moths · Insect hearing · Cochlear amplifier

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Introduction

The tympanal hearing organs of insects are formed by sensory elements called scolopidia, each consisting of a bipolar sensory neuron with a ciliated dendrite and two types of accessory cells, the scolopale cell and the attachment cell (see the review by Yack 2004). Noctuoid moths are unique because most species possess thoracic tympanal organs with only two auditory neurons (Eggers 1919). Among them, the notodontids are exceptional and particularly interesting. They have a bilateral pair of tympanal organs in their metathorax, each of which has just one auditory receptor neuron (Surlykke 1984). The single scolopidium is located in a thin filament that spans from the center of the tympanic membrane to cuticular anchoring structures (Surlykke 1984). As in other noctuoid moths, the hearing range of notodontids extends from 10 to 100 kHz (Surlykke 1984; Fullard 1984).

Hearing organs sensitive to low-intensity sound often employ nonlinear mechanical processing, regardless of the various anatomical and cellular specializations. Otoacoustic emissions (OAEs) are an indicator of such nonlinear mechanical processing and amplification in the inner ear of vertebrates. Distortion-product otoacoustic emissions (DPOAEs) are obtained during acoustic stimulation with two pure tones of distinct frequencies (*f*1 and *f*2, with

$f1 < f2$) and are a characteristic feature of sensitive hearing organs both in vertebrates (e.g. Brown and Gaskill 1990; Manley et al. 1993; Whitehead et al. 1996; Meenderink and van Dijk 2005) and in insects such as locusts (Kössl and Boyan 1998; Möckel et al. 2007) and noctuoid moths with two auditory neurons (Coro and Kössl 1998, 2001; Kössl and Coro 2006). In mammals, there is ample evidence that DPOAEs depend on a cochlear amplifier that involves force production by the motor protein prestin in the lateral cell wall of outer hair cells (e.g. Mills and Rubel 1994; Frank and Kössl 1996; Frolenkow et al. 1998; Liberman et al. 2002). In non-mammalian vertebrates, the hair bundle of sensory cells is most likely involved in active cochlear amplification and generation of otoacoustic emissions (Manley 2001). There is also recent evidence of hair bundle motors in mammals (Kennedy et al. 2005a, b; Chan and Hudspeth 2005).

The DPOAEs examined in insects show characteristics similar to those described in vertebrates, despite the fact that the insect sensory cells are not hair cells but primary mechanosensitive neurons with a single cilium (Gray 1960; Ghiradella 1971). Evidence that mechanosensory neurons in insects are indeed involved in mechanical sound amplification comes from studies in the antennal hearing organ of flies ("Johnston's organ"; Göpfert et al. 2005) and the tympanal organ of locusts (Möckel et al. 2007). In the present work with notodontids, we found that even ears with a single auditory neuron produce physiologically vulnerable DPOAEs. These are characterized by two distinct level-dependent components. The data support the proposal of Lukashkin et al. (2002) who have suggested that a single nonlinearity is sufficient to explain the vulnerable DPOAE growth functions with two components.

Materials and methods

Adult notodontids were collected with a light trap around midnight in the "Stadtwald" of Frankfurt am Main in May–June. The animals are scarce; hence our measurements concentrated on four specimens of *Ptilodon cucullina* [Denis and Schiffermüller 1775]. Additional experiments were also done with single preparations of *Drymonia obliterata* [Esper 1785] and *Phalera bucephala* [Linnaeus 1758]. All DPOAE-recordings took place immediately on the day after capture. To set up a moth preparation, the wings, legs and head were cut off, and the body was pinned dorsal side up to a cork platform atop a metal post. The physiological state of the preparations was assessed by the beat of the dorsal vessel, visible through the cuticle at the junction between thorax and abdomen.

The same acoustic coupler previously used to record DPOAEs from moths with two auditory neurons in each ear (Kössl and Coro 2006) was positioned 0.5–1 mm from the tympanic membrane. The coupler had a tip diameter similar to the size of the tympanic membrane and consisted of two adjacent conical tubes for stimulation and recording. The tympanal organ was stimulated with two pure tones of different frequency, $f1 < f2$, that were applied simultaneously. The $f1$ stimulus intensity was maintained 10 dB higher than that of the f2 stimulus. One coupler channel was connected to a ¼″ microphone (Brüel and Kjaer 4135), and two 1"microphone capsules (Microtech Gefell MK 103.1) served as speakers connected to the other coupler channel. All experiments were conducted in a soundproof chamber.

A Pentium PC with a Microstar 3000a/212 DSP board (A/D and D/A sampling rate of 250 kHz) was used for the generation of the acoustic stimuli and for FFT analysis of the microphone signal. A total of 100 responses to the 2 stimuli that had a constant phase relation were averaged before FFT analysis. The recording system was calibrated in situ for constant sound pressure level (SPL) at the microphone membrane using white noise (for details see Kössl et al. 1999). At the beginning of each experiment, a so-called DPOAE-audiogram was measured (see Coro and Kössl 1998) at a fixed $f2/f1$ frequency ratio of 1.09 and at levels of the two stimuli set to 55/45 or 60/50 dB SPL. This DPOAE audiogram allowed the selection of $f2$ frequencies at which the specimen produced large levels of $2f1–f2$ DPOAEs. At these selected $f2$ frequencies, the optimum frequency ratio $f2/f1$ was determined that elicited maximum emission levels. For the measurement of growth functions, the $f1$ frequency was adjusted to match the optimum frequency ratio.

To assess a possible physiological vulnerability of the $2f1–f2$ DPOAE in the ear of the notodontids, single drops of ethyl ether were applied topically on the dorsal surface of the thorax, near the auditory organ from which the DPOAEs were measured, after DPOAE-control measurements. Ethyl ether has been used to anaesthetize insects (Bellen et al. 1992). The application procedure did not change the position of the acoustic coupler relative to the tympanic membrane. Recordings of the growth functions began several minutes after the application of ether, while continuous recordings of DPOAEs with constant stimulus levels allowed an immediate assessment of the effects.

Results

As in vertebrates and in other insect species, the $2f1–f2$ DPOAE is dominant in the ears of *P. cucullina*. At higher stimulus levels, additional DPOAEs appear (Fig. 1). DPOAEs that were above the noise level (at ca. −15 dB SPL) were detected for stimuli in the frequency range from 35 to

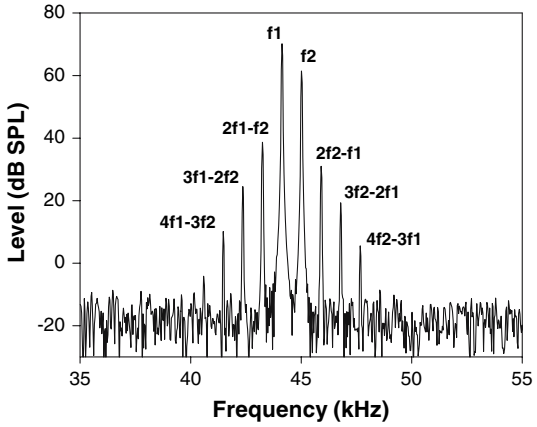

Fig. 1 Spectrum of distortion-product otoacoustic emissions (DPOAEs) measured at the tympanic membrane of the moth *Ptilodon cucullina* (Notodontidae). The *f*1 stimulus was 70 dB SPL and 44.1 kHz, and the *f*2 stimulus was 60 dB SPL and 45.0 kHz. Six different DPOAEs are clearly identified, together with the two primary stimuli

95 kHz. Growth functions of the 2*f*1–*f*2 DPOAE were obtained with *f*2 at 36, 45, 57, 66, 75, 84 and 95 kHz with *f*1 adjusted according to the optimum frequency ratio. The average optimum ratio was at 1.11(±0.07 SD). The shape of such growth functions (Fig. 2) is similar for different stimulus frequencies. There is a prominent notch (19.6 ± 4.1 dB depth; mean ± 1 SD), accompanied by a phase shift (119° ± 17°), in 20 of 26 growth functions of the 2*f*1–*f*2 DPOAE obtained in the four specimens of *P. cucullina* (Fig. 2). In the remaining six growth functions, the DPOAE level increased over the whole intensity range used, with no distinct notch or phase shift (e.g. Fig. 2a, e: solid squares). It is possible in these cases that the used stimulus levels were too low to reveal notches in the growth function. In the non-monotonic growth functions, the notch and the phase shift appear at a level of the *f*2 stimulus between 60 and 70 dB SPL (Fig. 2), and the minimal difference between the 2*f*1–*f*2 level and that of the *f*2 stimulus had a value of 19.5 ± 5.1 dB (range: 11.7–32.3 dB). This minimal difference was obtained for stimulus levels below the appearance of the notch. In addition, all growth functions exhibit a secondary discontinuity which was evident as a change of slope or a small notch <5 dB for *f*2 levels between 40 and 50 dB SPL (Fig. 2).

Most of the growth functions obtained in *P. cucullina* can be characterized by two distinct components. The presence of the notch allows the definition of a low- and a high-level component: *f*1 levels that evoke a DPOAE of around 0 dB SPL up to the *f*2 level just before the notch define the range of the low-level component (most of the growth functions in Fig. 2). The high-level component extends from the latter value up to the highest level of *f*2 used. The initial slope of the growth of the low-level component, determined at 0 dB SPL emission level, is 1.6 ± 0.6 dB/dB (n = 23 trials; range 0.80–3.10).

The effects of ethyl ether were assessed by comparing the growth functions obtained before and at intervals after application of single drops of ethyl ether (Fig. 3a–d). In addition, in several cases we recorded DPOAEs continuously under constant stimulus conditions to document fast changes in DPOAE-amplitude occuring immediately after ether application (Fig. 3e). To avoid the possibility that such fast changes distort the measured growth functions, we started recording at least 8 min after an ether application. The long-term effect of ether on the growth functions was always a slow decrease of emission amplitude. The effect was generally stronger on the low-level component than on the high-level component (Fig. 3b, c, d). In the three specimen where growth functions were measured during ether application, the low-level component (*f*2-levels below the notch) was reduced by maximally 37.7 ± 1.6 dB, the high-level component (*f*2 levels at or above the notch) was reduced by maximally 25 ± 7.5 dB. The amount of ether to elicit this long-term effect was variable between animals [two drops in the first specimen (Fig. 3a), nine drops in the second specimen (Fig. 3b), ten drops in the third specimen (Fig. 3c, d)]. Comparable result were also obtained in the two other species of notodontids tested (*Drymonia obliterata, Phalera bucephala*).

The continuous distortion recordings revealed that there were additional short-term effects of ether such as a brief decrease or increase of the distortion level or biphasic effects (Fig. 3e). The most frequent short-term effect of ether was a decrease of the DPOAE level followed by partial or full recovery. In 18 of 23 ethyl ether applications, there was a short-term decrease of the DPOAE, in 3 cases the DPOAE level increased, and in 2 cases the changes were biphasic (Fig. 3e).

Discussion

The DPOAEs recorded from notodontid ears, having only one auditory neuron, show similarities with those obtained in the much more complex locust ear (Kössl and Boyan 1998; Möckel et al. 2007), as well as with those well-known in vertebrate ears (Mills and Rubel 1996). These similarities include: (1) the 2*f*1–*f*2 distortion is dominant following a stimulation paradigm in which the level of *f*1 is higher than that of *f*2; (2) growth functions of the 2*f*1–*f*2 distortion are often non-monotonic and show a notch accompanied by a phase shift at intermediate sound levels; (3) in non-monotonic growth functions, the notch separates a low-level from a high-level component, and the low-level component is physiologically more vulnerable. We recorded DPOAEs at stimulus frequencies up to 95 kHz,

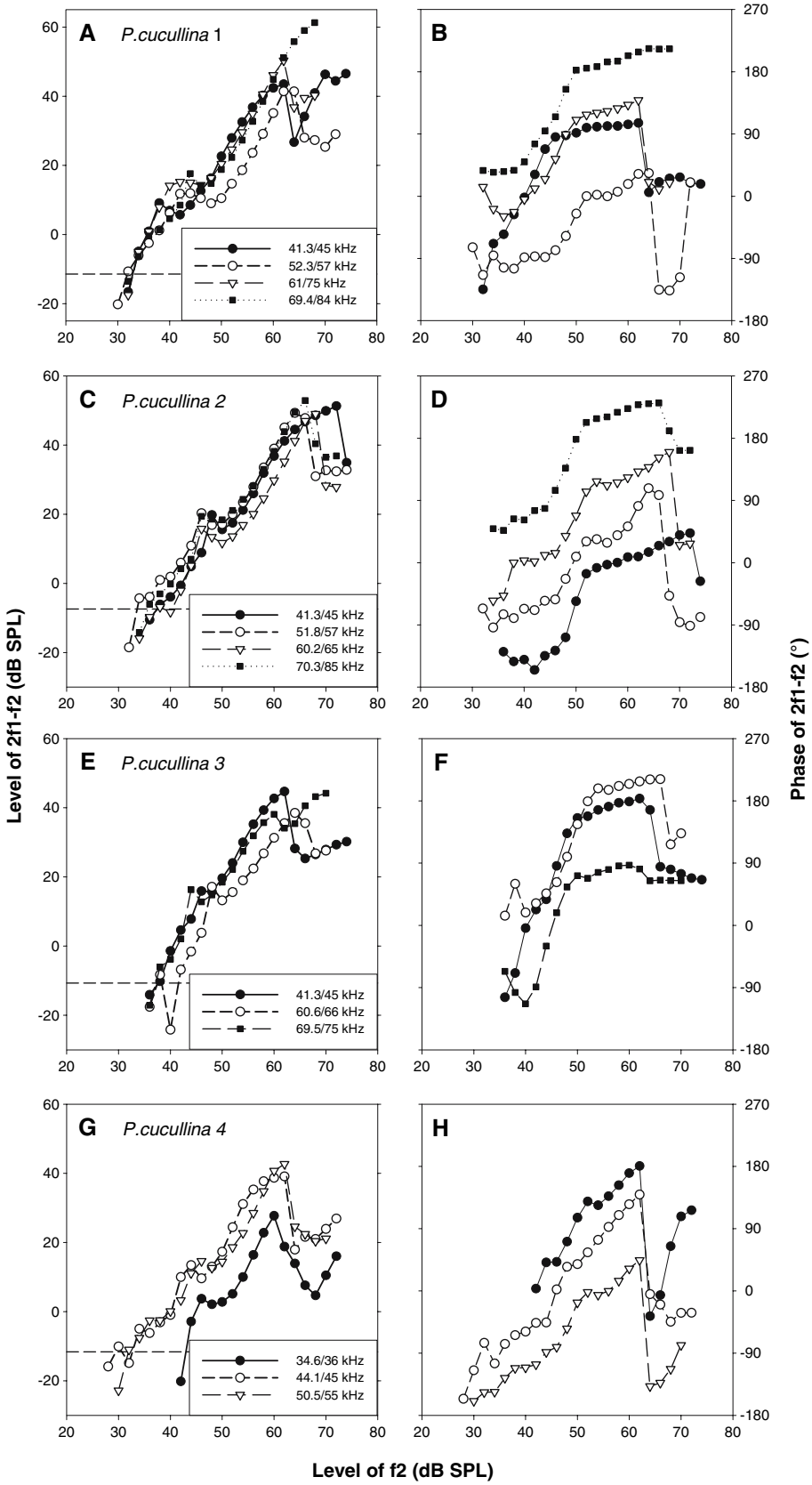

Fig. 2 Growth of the level of the 2*f*1–*f*2 DPOAE (*left side*) and changes of the corresponding DPOAE phase (*right side*) with increasing *f*2 levels in four specimens of *P. cucullina*. The level of *f*2 was always 10 dB below that of *f*1. For each specimen, level growth curves obtained with several different stimulation frequencies are shown (see *inset*). The dashed horizontal lines give the noise level of the measurements expressed as mean ± 1 SD. The DPOAE growth functions are generally characterized by a pronounced notch in the level of distortion coupled with a sudden change of DPOAE phase for *f*2 levels between 60 and 70 dB SPL. Two of the displayed growth functions (**a**, **e** *filled squares*) do not exhibit a notch and have a more monotonic growth characteristic. All growth functions have a secondary minimum or a change of slope at *f*2 levels between 40 and 50 dB SPL

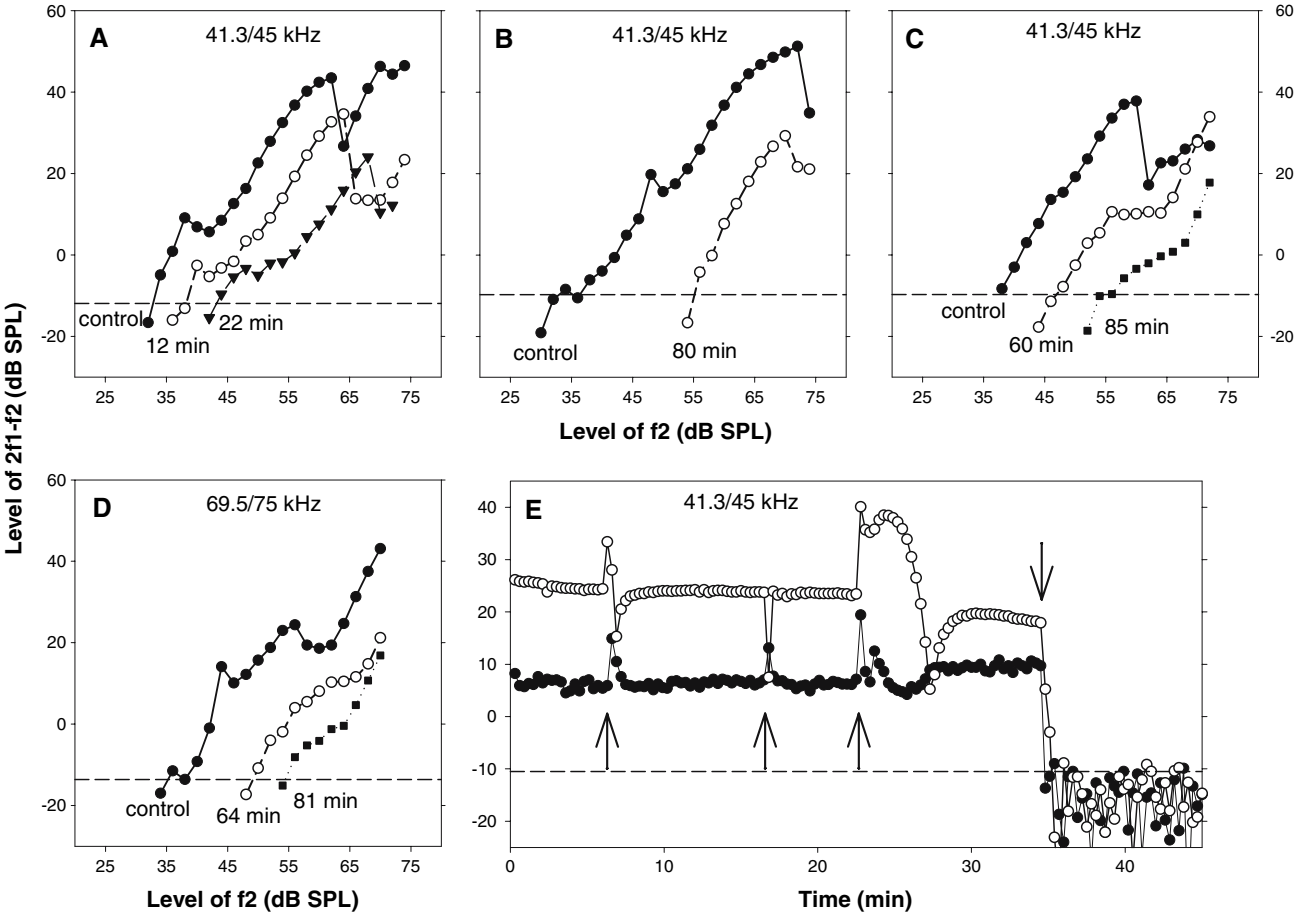

Fig. 3 Effects of topical application of drops of ethyl ether on dorsal part of the thorax of *P. cucullina*. Growth of the 2*f*1–*f*2 DPOAE level before and after application of ethyl ether in three specimens of *P. cucullina*. The used frequency combinations are given above each figure. In one specimen two different frequency combinations were tested (**c**, **d**). The *dashed horizontal lines* show the range of the noise expressed as mean ± 1 SD. The decrease in emission level was induced by application of two drops (**a**), nine drops (**b**), and ten drops (**c**, **d**) of ether. **e** Continuous recording of 2*f*1–*f*2 distortion-product in the fourth specimen at 2 different levels: 60/50 dB SPL (*filled circles*) and 75/65 dB SPL (*open circles*). *Arrows* show the time points of application of the ethyl ether. The first three applications of ether in this specimen evoked short-term and reversible increases or decreases of the DPOAE level while the fourth application completely abolished the DPOAE responses to both stimulus levels

which is the highest value reported so far for insect otoacoustic emissions. The hearing range of notodontids includes these frequencies (Surlykke 1984; Fullard 1984), and this may indicate that nonlinear ear mechanics are functional at highest frequencies.

Modes of nonlinearity and physiological vulnerability

The initial slope of the low-level component of 1.6 is comparable to those in moths with more than one auditory cell (*E. affinis*: slope 1.9, Coro and Kössl 2001) and slightly higher than in some hearing organs with considerably more receptor cells in which a comparable stimulation paradigm was used (locust: slope 0.46–1.48, Kössl and Boyan 1998; bobtail lizard: 0.4–1.3, Manley et al. 1993; human: 0.6–1.4, Abdala 2000). The slope of the growth functions is dependent on the type of nonlinearity involved, but its indicative value is rather restricted and it does not allow speculation about active or passive mechanisms. A slope of close to 2 could be indicative of a passive nonlinearity described by the power law (see Mills and Rubel 1994) or of any other nonlinearity as long as the gain of a putative mechanical amplification mechanism is constant and level-independent for a restricted input level range. Initial slopes of DPOAE growth functions close to 2 were also found in sensitive mammalian preparations (gerbil: Mills and Rubel 1994, 1996; human: Popelka et al. 1993, Fig. 2).

In mammals, a measure of the gain of cochlear amplification can be obtained by selective manipulation of the endocochlear potential and a detailed assessment of the resulting horizontal shift of the DPOAE growth functions (Mills and Rubel 1994, 1996). In *P. cucullina*, after application of ethyl ether, the growth functions shift by about 20 dB, which is comparable to the shift seen in another moth

species with more than one cell (Coro and Kössl 2001) and less than that seen in mammals (Mills and Rubel 1996). The observation that DPOAEs in notodontids are physiologically vulnerable indicates that cellular metabolism is necessary for sensitive function of the tympanal organ, but of course does not necessarily imply that an active mechanical amplifier is involved which could be localized in the receptor neuron itself. Direct evidence that scolopidial organs are indeed capable of active vibration and amplification comes from studies in the Johnston's organ of mosquitoes and flies (Göpfert and Robert 2001, 2003; Göpfert et al. 2005). Putative auditory motor proteins in insects are prestin-homologues (Weber et al. 2003) or proteins of the transduction apparatus (Göpfert and Robert 2003). Conclusive proof of active amplification in the moth tympanal organ is still missing. The present data do, however, show that the nonlinear mechanical properties of the single receptor neuron organ and its vulnerability is comparable to more complex tympanal organs and also to vertebrate ears.

A single nonlinear element?

As pointed out by Lukashkin and Russell (1999) and Lukashkin et al. (2002) for the mammalian cochlea, a single nonlinear element, namely an active amplifier with a compressive input/output characteristic, could be sufficient to produce both low- and high-level DPOAE components and also their differential vulnerability. These authors describe the nonlinearity by a Boltzman function derived from transduction currents of single hair cells. According to their model, an interaction and cancellation between the nonlinear activities of different groups of outer hair cells is not necessary to produce level-dependent growth function components and corresponding phase shifts. It has been shown in a moth species with more than one receptor cell that the level growth behaviour of DPOAEs is consistent with a Boltzman function (Kössl and Coro 2006). It is tempting to apply this concept also to the notodontid ear with its single receptor neuron. Hence the present data would directly support the proposal of Lukashkin et al. (2002). There is, however, an additional secondary discontinuity at lower stimulus levels in the notodontid DPOAE level growth functions which is not seen in mammalian data. This could be due to a shift or asymmetry of the nonlinear Boltzman function as suggested by Kössl and Coro (2006). In the model of Lukashkin, cochlear amplification is saturated at high input levels that correspond to the high-level DPOAE component. Consequently, a change of gain of the cochlear amplifier induced by physiological manipulations does not affect the high-level component as strongly as the low-level component. The same reasoning would explain that the effects of ether are stronger on low-level DPOAE components in the notodontids. However, even if it is apparent that only one scolopidium can contribute to putative nonlinear amplification in the notodontids, it is not clear where exactly the putative nonlinear element is located and what role the accessory cells play in the mechanical nonlinearity. If the situation in tympanal organs is comparable to that of vertebrate hearing organs, the most likely source of nonlinearity is a combination of a nonlinear (mechano-electrical) transduction channel coupled to a force generator. In vertebrates, force generation may either depend on motile proteins located in the cilium (Kennedy et al. 2005a, b) or in the soma of the sensory cell (such as prestin-based motility in mammals; review: Dallos and Fackler 2002). As shown by Göpfert et al. (2006), nonlinear force production in Johnston's organ of *Drosophila* can be influenced by disrupting putative transducer channel proteins such as NompC and vanilloid proteins that may regulate amplification, but it remains unclear whether the transducers themselves were in fact disrupted.

To resolve this issue in tympanal organs, a more specific manipulation of the sensory cell is required than is possible with topic application of ether. That the sensory cells are indeed involved in emission generation was demonstrated in the hearing organ of locusts (Müller's organ) by Möckel et al. (2007) who showed that selective ablation of groups of sensory cells specifically affects DPOAE in the frequency range that is processed by these cell groups.

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References

Abdala C (2000) Distortion product otoacoustic emissions (2*f*1-*f*2) amplitude growth in human adults and neonates. J Acoust Soc Am 107:446–456

Bellen HJ, Vaessin H, Bier E, Kolodkin A, D'Evelyn D, Kooyer S, Jan YN (1992) The *Drosophila couch potato* gene: an essential gene required for normal adult behavior. Genetics 131:365–375

Brown AM, Gaskill SA (1990) Measurement of acoustic distortions reveals underlying similarities between human and rodent mechanical responses. J Acoust Soc Am 94:809–816

Chan DK, Hudspeth AJ (2005) Ca^{2+} driven nonlinear amplification by the mammalian cochlea *in vitro*. Nat Neurosci 8:149–155

Coro F, Kössl M (1998) Distortion-product otoacoustic emissions from the tympanic organ of two noctuoid moths. J Comp Physiol A 183:525–531

Coro F, Kössl M (2001) Components of the 2*f*1-*f*2 distortion-product otoacoustic emission in a moth. Hear Res 162:126–133

Dallos P, Fackler B (2002) Prestin, a new type of motor protein. Nat Rev Mol Cell Biol 3:104–111

Eggers F (1919) Das thorakale bitympanale Organ einer Gruppe der Lepidoptera Heterocera. Zool Jb (Anat) 41:273-376

Frank G, Kössl M (1996) The acoustic two-tone distortions 2*f*1-*f*2 and *f*2-*f*1 and their possible relation to changes of the gain and operating point of the cochlear amplifier. Hear Res 98:104–115

Frolenkow GI, Belyantseva IA, Kurc M, Mastroianni MA, Kachar B (1998) Cochlear outer hair cell electromotility can provide force for both low and high intensity distortion product otoacoustic emission. Hear Res 126:67–74

Fullard JH (1984) External auditory structures in two species of neotropical notodontid moths. J Comp Physiol A 155:625–632

Ghiradella H (1971) Fine structure of the noctuid ear. I. The transducer area and connection to the tympanic membrane in *Feltia subgothica* (Haworth). J Morphol 134:21–45

Göpfert MC, Robert D (2001) Active auditory mechanics in mosquitoes. Proc R Soc Lond Ser B 268:333–339

Göpfert MC, Robert D (2003) Motion generation by Drosophila mechanosensory neurons. Proc Natl Acad Sci USA 100:5514–5519

Göpfert MC, Humphris ADL, Albert JT, Robert D, Hendrich O (2005) Power gain exhibited by motile mechanosensory neurons in *Drosophila* ears. Proc Natl Acad Sci USA 102:325–330

Göpfert MC Albert JT Nadrowski B Kamikouchi A (2006) Specification of auditory sensitivity by Drosophila TRP channels. Nat Neurosci 9:999–1000

Gray EG (1960) The fine structure of the insect ear. Phil Trans R Soc Lond B 243:75–94

Kennedy HJ, Evans MG, Crawford AC, Fettiplace R (2005a) Depolarization of cochlear outer hair cells evokes active bundle motion by two mechanisms. J Neurosci 26:2757–2766

Kennedy HJ, Crawford AC, Fettiplace R (2005b) Force generation by mammalian hair bundles supports a role in cochlear amplification. Nature 433:889–883

Kössl M, Boyan GS (1998) Acoustic distortion products from the ear of a grasshopper. J Acoust Soc Am 104:326–335

Kössl M, Coro F (2006) L_1,L_2 maps of distortion product otoacoustic emissions from a moth ear with only two auditory receptor neurons. J Acous Soc Am 120:3822–3831

Kössl M, Mayer F, Frank G, Faulstich H, Russell IJ (1999) Evolutionary adaptations of inner ear function in Jamaican mormoopid bats. J Comp Physiol A 185:217–228

Liberman MC, Gao J, He DZZ, Wu X, Jia S, Zuo J (2002) Prestin is required for electromotility of the outer hair cell and for the cochlear amplifier. Nature 419:300–304

Lukashkin AN, Russell IJ (1999) Analysis of the *f*2-*f*1 and 2*f*1-*f*2 distortion components generated by the hair cell mechanoelectrical transducer: Dependence on the amplitudes of the primaries and feedback gain. J Acoust Soc Am 106:2661–2668

Lukashkin AN, Lukashkina VA, Russell IJ (2002) One source for distortion product otoacoustic emissions generated by low- and high-level primaries. J Acoust Soc Am 111:2740–2748

Manley GA (2001) Evidence for an active process and a cochlear amplifier in nonmammals. J Neurophysiol 86:541–549

Manley GA, Köppl C, Johnstone BM (1993) Distortion-product otoacoustic emissions in the bobtail lizard. I. General characteristics. J Acoust Soc Am 93:2820–2833

Meenderink SWF, van Dijk P (2005) Characteristics of distortion product otoacoustic emissions in the frog from L_1, L_2 maps. J Acoust Soc Am 118:279–286

Mills DM, Rubel EW (1994) Variation of distortion product otoacoustic emissions with furosemide injection. Hear Res 77:183–199

Mills DM, Rubel EW (1996) Development of the cochlear amplifier. J Acoust Soc Am 100:428–441

Möckel D, Seyfarth EA, Kössl M (2007) The generation of DPOAEs in the locust ear is contingent upon the sensory neurons. J Comp Physiol A (in press)

Popelka GR, Osterhammel PA, Nielsen LH, Rasmussen AN (1993) Growth of distortion product otoacoustic emissions with primary-tone level in humans. Hear Res 71:12–22

Surlykke A (1984) Hearing in notodontid moths: a tympanic organ with a single auditory neurone. J Exp Biol 113:323–335

Weber T, Göpfert MC, Winter H, Zimmermann U, Kohler H, Meier A, Hendrich O, Rohbock K, Robert D, Knipper M (2003) Expression of prestin-homologous solute carrier (SLC26) in auditory organs of nonmammalian vertebrates and insects. Proc Natl Acad Sci USA 100:7690–7695

Whitehead ML, Lonsbury-Martin BL, Martin GK, McCoy MJ (1996) Otoacoustic emissions: animal models and clinical observations. In: Van de Water TR, Popper AN, Fay RF (eds) Clinical aspects of hearing. Springer, Berlin, pp 199–258

Yack J (2004) The structure and function of auditory chordotonal organs in insects. Microsc Res Tech 63:315–337