Biophysics, neural processing and robotics of the lizard ear, a highly directional sensor

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The ear of lizards shows strongly directional responses with up to 40 dB differences in sensitivity to ipsi- and contralateral stimulation. The directionality is generated by a simple principle: strong acoustical coupling of the eardrums through the large mouth cavity. Our laser vibrometry measurements show that the lizard ear is a two-input system with approximately 0 dB contralateral transmission gain in a 2 kHz frequency band. This transmission is boosted by resonances in the large, open tympanic cavities. Probably because of these resonances, the interaural delay is approximately three times larger than the arrival-time differences at the lizard eardrums.

Since already the ear is directional, the subsequent neural processing may be much simpler than in mammals, for example, where directionality is based on neural computation. Our neurophysiological experiments show that binaural comparison is based on contralateral inhibition with no apparent segregation of time and intensity processing. This simple computation generates a strongly directional lateralization that is sufficient to orient the animal. This has been shown by robot simulations, where the ear is modelled by a simple three-impedance acoustical analog. Implementation of the model in a digital signal processor and subsequent neural processing based on binaural comparison produces a robust directional response.

INTRODUCTION

To determine the direction to a sound source is fundamentally important for all hearing organisms. Not surprisingly, a large amount of auditory processing is dedicated to processing of directional cues. In most vertebrates, an essential element of directional processing is binaural comparisons. In the mammals and some birds, most notably the barn owl, binaural comparisons of interaural time differences (ITD) and interaural level differences (ILD) are the most important types of binaural processing and are segregated in separate time and intensity pathways in the central nervous system (CNS).

In mammals and some birds the two eardrums are independent receivers, also called pressure receivers, and the ears are only directional at high frequencies, where the head and external ears are casting a sound shadow. In other animals, however, directionality is generated by acoustical coupling of the two eardrums, so sound can reach both sides of the eardrum. Such ears are inherently directional, also at low

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frequencies, where there is no sound diffraction, since the eardrum motion is driven by the phase difference between the direct sound and the indirect sound (arriving from the contralateral eardrum). These so-called pressure difference receiver ears are found in anurans (frogs and toads) and some birds (Feng and Christensen-Dalsgaard 2007), but the most extreme example of this kind of directionality has been demonstrated recently in lizards (Christensen-Dalsgaard and Manley 2005, 2008, review in Christensen-Dalsgaard 2005). In the present paper I will briefly review the directional processing of the lizard ear. Also, the robust directionality of the ear has led to a straightforward implementation in a sound localizing robot, and the construction and performance of the robot will also be reviewed here.

THE LIZARD EAR

Surprisingly, the tympanic ears of all the major terrestrial vertebrate groups, i.e., amphibians, turtles, lizards, archosaurs (birds, dinosaurs, crocodiles) and mammals evolved independently from atympanate ancestors in the Triassic (approximately 250 mya), although the stapes is homologous in all the groups (Clack 1997, Christensen-Dalsgaard and Carr 2008), so the lizard ear constitutes an independent 'experiment in hearing'.

The anatomy of the lizard ear has been extensively studied by Wever (1978) and Manley (1989). Most lizards have very sensitive middle ears with thin eardrums and one middle ear bone, the stapes or columella. No external ears are present, but some species have a short ear canal. A very conspicuous feature is that the middle ear bones are exposed in the mouth cavity, i.e. the middle ear cavities are completely open; this feature is the basis of the strong acoustical coupling of the lizard ear.

The general sensitivity of the auditory system is generally comparable to the sensitivity of birds as shown by recent auditory brainstem response (ABR) measurements (Brittan-Powell *et al.*, 2010) with maximal sensitivity at 1-4 kHz and strongly reduced sensitivity above 10 kHz.

Measurements of eardrum vibrations using laser Doppler vibrometry and free-field stimulation showed that the ears of seven different lizard species were highly directional (Christensen-Dalsgaard and Manley 2005, 2008, see example in Fig. 1a). The directivity is asymmetrical with up to 40 dB ipsi-contralateral difference in a 2 kHz frequency band (center frequency depends on the size of the animal, in this small animal (the house gecko *Hemidactylus*, head width 1 cm) it is 3 kHz) and can be abolished by shielding one of the eardrums with Vaseline (Fig. 1b). This suggests that interaural coupling is important for the directionality. Subsequently, in four lizard species we measured the interaural coupling directly by using a method devised by Michelsen and Rohrseitz (1995) by measuring the eardrum vibration transfer functions in response to ipsilateral and contralateral local stimulation (Christensen-Dalsgaard and Manley 2008). The direct transmission across the head was shown to be insignificant, so the ratio of contralateral divided by ipsilateral transfer function is a measure of the interaural transmission gain, i.e. the sound transmitted via the contralateral eardrum in proportion to the direct sound transmitted via the ipsilateral eardrum. The interaural transmission gain for *Hemidactylus* is shown in Fig. 1c and 1d. The interaural transmission gain is surprisingly high, especially in the frequency band of maximal directionality and exceeding 0 dB at the peak directional frequency. This is extraordinary, since sound then arrives at the internal side of the eardrum at the same or higher level than the 'direct' sound arriving at the external side of the eardrum. Naturally, this strong coupling can provide complete cancellation of eardrum motion at certain phase differences, i.e. directions. Furthermore, the approximately linear phase-frequency relationship shown in Fig. 1d shows that the interaural transmission gain has a large transmission delay. The slope of curve is approximately 1.1 rad/kHz, corresponding to a delay of 185 µs or approximately three times the propagation delay across the head. This delay amplifies the phase difference between sound at the two sides of the eardrum and increases its directivity. To summarize, this study showed that the ear is a two-input system with strong coupling between the two eardrums.

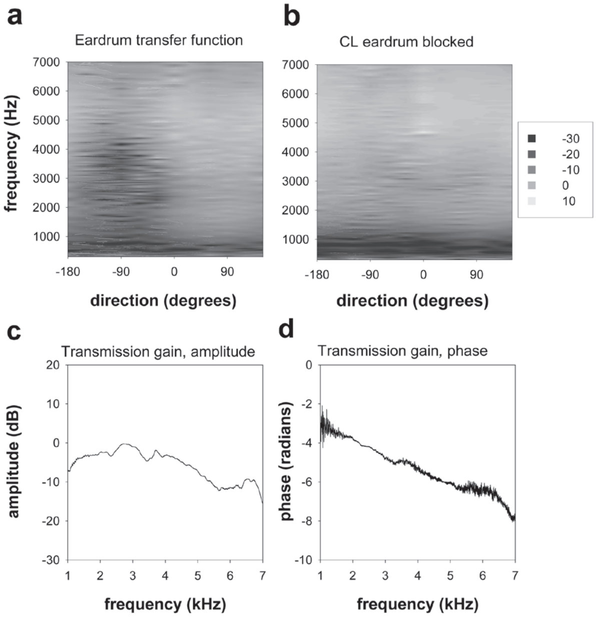

Fig. 1: Laser vibrometry measurements from the house gecko eardrum. a: Eardrum vibration transfer function (x-axis: direction, positive angles ipsilateral; y-axis frequency, grayscale: amplitude in dB re 1 mm/s/Pa). b: transfer function after occluding one ear with Vaseline. C, D: Interaural transmission gain amplitude (c) and phase (d); see text for further details. From Christensen-Dalsgaard and Manley 2008, redrawn.

MODELLING THE LIZARD EAR

The two-input lizard ear can be represented by a three-impedance analog electrical circuit (Fletcher 1992) (Fig. 2). The impedances can be either calculated from anatomical measurements (Christensen-Dalsgaard and Manley 2005) or calculated from the transmission gain measurements (Christensen-Dalsgaard and Manley 2008). In both cases, the model directionality is generally similar to the measured values at lower frequencies, but deviates at frequencies above 5 kHz . More sophisticated finite-element modeling based on scans of the internal cavities also shows large directionality and transmission delay (Vossen *et al*., 2010).

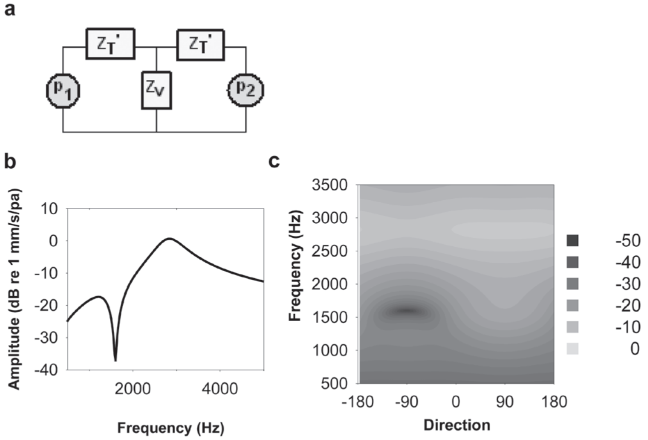

Fig. 2: Analog model of the lizard ear, based on Fletcher (1992). The model circuit is shown in panel a, assuming connection of the two tympana with impedances Z_T‘ through a central cavity Z_V. Panel b and c shows model calculations, in b the ipsilateral (dotted line) and contralateral spectrum, in c the model eardrum transfer function (in dB re 1 mm/s/pa) as a function of direction (x-axis) and frequency (y-axis). Compare with Fig. 1a. From Christensen-Dalsgaard and Manley 2005.

The internally coupled ear of lizards generates a strongly directional response of the tympanum. The response of auditory nerve fibers in the Tokay gecko accurately reflects the eardrum response, and with dichotic stimulation the nerve response is modulated by ITD, most likely caused by cancellation of eardrum vibrations. Also, the neural response to free-field stimulation reflects the strong directionality of the eardrum shown in the laser vibrometry measurements. Therefore, directionality becomes a feature of every neuron in the auditory pathway. The neural processing of directional information is largely unknown. However, using dichotic stimulation and blocking interaural transmission, binaural interactions could be identified in the first-order nucleus magnocellularis neurons and presumably in the superior olivary nucleus, and these nuclei seem to process low and high frequencies, respectively (Christensen-Dalsgaard and Carr 2008). These binaural interactions were complex, showing both inhibition and excitation and depending on both ITD and ILD. The further neural processing of binaural cues is unknown, but strongly directional responses to free-field stimulation have been recorded from the midbrain Torus Semicircularis in the tokay gecko (Manley 1981).

Since a part of the binaural processing is performed by the acoustical coupling instead of by neural interaction our assumption is that the subsequent neural processing is much simpler than in animals with uncoupled ears. A simple model of neural processing assuming neural subtraction of the ipsilateral and contralateral input (by EI neurons in the CNS) produces a strong sharpening, because the eardrum response is highly asymmetric across the midline (Fig 3). The subtraction produces a gradient of up to 40 dB across the frontal directions (Christensen-Dalsgaard and Manley 2005, 2008), and since the model does not incorporate timing differences, the real neural response of EI neurons may be even stronger. The demarcation of the midline can give a very precise steering towards sound sources, as shown by the robotics simulations in Fig. 3.

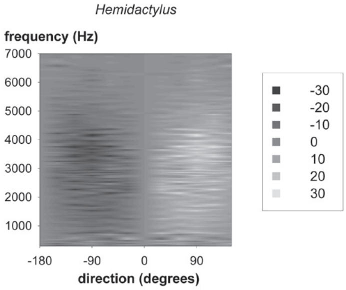

Fig. 3: A model of an EI neural response. The response is created by dividing the response (i.e. subtracting dB values) shown in Fig 1a by its mirror reflection across the midline (0º), simulating the response of the contralateral ear. Since the neural response rate is a linear function of level in dB, this is a model of neural subtraction. The dB scale now is the dB difference between the two transfer functions, other details same as in Fig. 1a. Note the steep gradient along the frontal axis, created by the asymmetrical directivity. From Christensen-Dalsgaard and Manley 2008, redrawn.

The robotic simulations were based on the very simple acoustical model of the ear (Fig 2.) and a neural comparison as outlined above. After filtering by the acoustical model, the input from the two ears are compared binaurally, leading to stronger excitation of one ear than the other. In the latest version of the robot (Shaikh *et al.*, 2009) the level of excitation of each binaural cell is directly driving the left and right robot motors. The acoustical model as well as the neural interaction is realized either on a digital signal processor or on a field programmable gate array.

From these robotic experiments using the ear model, a model of neural comparison based on bilateral EI neurons (Fig 3) and a simple decision rule, that the robot steers towards the most excited EI neuron, it can be shown that a moving animal equipped with the directional eardrums and just using lateralization is perfectly able to orient to sound and to locate the sound source in experiments with continuous sound stimulation (i.e, closed-loop experiments, (Zhang *et al*., 2006). According to the physiological data from frogs this simple lateralization can definitely be realized in the CNS of frogs (Christensen-Dalsgaard and Kanneworff, 2005) and probably also in lizards. This suggests that an ‘encoding’ of sound direction or a spatial map is not necessary for adequate performance. Also, it is even possible with a lateralization mechanism to have a graded directional response. In a recent robot experiment, this was realized by interfacing the output of the bilateral EI neurons with the motors in a Braitenberg vehicle, where the level of excitation of the EI-neurons controlled the motor output directly (Shaikh *et al*., 2009), i.e. the larger the interaural difference, the stronger turning movement. If the response time is short enough this configuration will produce a true angle response.

CONCLUSION

In conclusion, the robot experiments have been an important tool for understanding the biological function of the lizard ear. This very simplified model lends itself to technological uses, but more importantly, the robotic analysis suggests that it might be fruitful to study sound localization from the motor or ‘output’ side instead of, as usually, from the sensory or ‘input’ side. The view from the input side will be how sensory stimuli are ‘encoded’ in the nerve responses, leading to a representation in the CNS. However, the view from the output side will be that no such code necessarily exists; what is needed is the network activity that produces the output in a set of motoneurons appropriate for steering the animal appropriately.

REFERENCES

Brittan-Powell, E. F., Christensen-Dalsgaard, J., Tang, Y., Carr, C. E., and Dooling, R. (**2010**). “The auditory brainstem response in two lizard species,” J. Acoust. Soc. Am. *in press*.

Christensen-Dalsgaard, J. (**2005**). “Directional hearing in non-mammalian tetrapods,” in *Sound Source Localization* edited by A. N. Popper and R. R. Fay (Springer-Verlag, New York), pp. 67-123.

Christensen-Dalsgaard, J., and Carr, C. E. (**2008**). “Evolution of a sensory novelty: the tympanic ears and the associated neural processing,” Brain Res. Bull. **75**, 365-370.

Christensen-Dalsgaard, J., and Kanneworff, M. (**2005**). “Binaural interactions in the frog dorsal medullary nucleus,” Brain Res. Bull. **66**, 522-525.

Christensen-Dalsgaard, J., and Manley, G. A. (**2005**). “Directionality of the lizard ear,” J. Exp. Bio. **208**, 1209-1217.

Christensen-Dalsgaard, J., and Manley, G. A. (**2008**). “Acoustical coupling of lizard eardrums,” JARO **9**, 407-416.

Clack, J. A. (**1997**). “The evolution of tetrapod ears and the fossil record,” Brain. Behav. Evol. **50**, 198-212.

Feng, A. S., and Christensen-Dalsgaard, J. (**2007**). "Interconnections between the ears in nonmammalian vertebrates," in *The Senses: A comprehensive reference* edited by A. Basbaum A. *et al*. (Elsevier), vol 3, p. 217-224.

Fletcher, N. H. (**1992**). *Acoustic systems in biology* (Oxford University Press, Oxford).

Manley, G. A. (**1981**). "A review of the auditory physiology of the reptiles," Prog. Sens. Physiol. **2**, 49-134.

Manley, G. A. (**1990**). *Peripheral Hearing Mechanisms in Reptiles and Birds* (Springer-Verlag, New York).

Manley, G. A. (**2002**). "Evolution of structure and function of the hearing organ of lizards," J. Neurobiol. **53**, 202-211.

Michelsen, A., and Rohrseitz, K. (**1995**) "Directional sound processing and interaural sound transmission in a small and a large grasshopper," J Exp Biol **198**, 1817-1827.

Shaikh, D., Hallam, J., Christensen-Dalsgaard, J., and Zhang, L. (**2009**) "A Braitenberg Lizard: Continuous Phonotaxis with a Lizard Ear Model," in *Lecture Notes in Computer Science 5602* (Springer-Verlag, New York), pp. 439-448.

Vossen, C., Christensen-Dalsgaard, J., and van Hemmen, J. L. (**2010**). "An analytical model of the lizard pressure-gradient receiver ear," J. Acoust .Soc. Am., *in press*.

Wever, E. G. (**1978**). *The Reptile Ear* (Princeton University Press, Princeton).

Zhang, L., Hallam, J., and Christensen-Dalsgaard, J. (**2006**). "Modelling the lizard auditory periphery," in *From animals to animats 9. Proceedings of 9th international conference on simulation of adaptive behaviour*, edited by S. Nolfi *et al*. (Springer), pp. 65-76.