

Research paper

Do Swiftlets have an ear for echolocation? The functional morphology of Swiftlets' middle ears

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Abstract

The Oilbird and many Swiftlet species are unique among birds for their ability to echolocate. Echolocaters may benefit from improved hearing sensitivity. Therefore, morphological adaptations to echolocation might be present in echolocating birds' middle ears. We studied the functional morphology of the tympano–ossicular chain of seven specimens of four echolocating Swiftlet species and one specimen each of five non-echolocating species. Three dimensional (3D) reconstructions were made from micro-Computer-Tomographic (μ CT) scans. The reconstructions were used in functional morphological analyses and model calculations. A two dimensional (2D) rigid rod model with fixed rotational axes was developed to study footplate output-amplitudes and to describe how changes in the arrangement of the tympano–ossicular chain affect its function. A 3D finite element model was used to predict ossicular-chain movement and to investigate the justification of the 2D approach. No morphological adaptations towards echolocation were found in the middle-ear lever system or in the mass impedance of the middle ear. A wide range of middle-ear configurations result in maximum output-amplitudes and all investigated species are congruent with these predicted best configurations. Echolocation is unlikely to depend on adaptations in the middle ear tympano–ossicular chain.

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1. Introduction

Morphological adaptations to echolocation have been studied extensively in mammals (primarily bats and cetaceans) (e.g., Bradbury and Vehrencamp, 1998, and references therein), but not in birds. The only known bird

species that are able to echolocate are the South American Oilbird (*Steatornis caripensis*) (e.g., Griffin, 1953; Konishi and Knudsen, 1979; Pye, 1980; Suthers and Hector, 1985) and several species of Southeast Asian Swiftlets (*Collocaliini*), i.e. *Aerodramus* spp. (e.g., Griffin and Suthers, 1970; Fenton, 1975; Medway, 1967; Smyth, 1979; Suthers and Hector, 1982) and *Collocalia troglodytes* (Price et al., 2004; Thomassen et al., 2005). The echo clicks of the Oilbird are single or double clicks with frequencies between approximately 0.5 and 15 kHz (Suthers and Hector, 1985). The clicks of Swiftlets are also of single as well as double click design (Suthers and Hector, 1982; Thomassen et al., 2004) and range roughly between 1 and 10 kHz (Thomassen and Povel, 2006). Echolocation in *Steatornis caripensis* and *Collocaliini* is primarily used to navigate in

Abbreviations: FE, finite element; F_{coch} , cochlear resistance; F_{in} , input force; FL, force lever; FP, footplate; FP_x , position of the footplate along the x -axis; OW, oval window; RL, resistance lever; SPL, sound pressure level; S_x , position of the scapus–extracolumella along the x -axis; S_y , position of the scapus–extracolumella along the y -axis

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the darkness of their roosting and nesting caves, and not to locate food. *Steatornis caripensis* is a fruit eater, but only very occasionally echolocates outside a cave, while Swiftlets locate their insect prey visually. The wavelengths of the frequencies used to echolocate are too long to detect small prey items. Although several studies exist on echolocation acuity (e.g., Fenton, 1975; Fullard et al., 1993; Griffin and Suthers, 1970; Griffin and Thompson, 1982; Smyth and Roberts, 1983), there is little knowledge about morphological characteristics that make echolocation possible. The physiology of syringeal click production has been studied in both the Oilbird (Suthers and Hector, 1985) and the Swiftlets (Suthers and Hector, 1982). The present paper is one in a series of three (Thomassen et al., unpublished) in which the main components of the echolocation system – syrinx, ear, and central nervous system – are investigated. In this paper we will concentrate on the middle ear. We studied and compared the functional morphology of the tympano–ossicular chain in Swifts and Swiftlets and examined whether morphological adaptations towards echolocation are present.

As a device that transduces sound waves from air to oscillations in the cochlear fluid, the middle ear may have played a crucial role in the evolution of echolocation. The frequency range that can be detected has long been thought to be mainly determined by the middle ear. However, Ruggero and Temchin (2002) made clear that middle ears may well be wide-band transformers, spanning (and possibly exceeding) all frequencies of hearing. Instead, it is the cochlea that sets the frequency detection limit. It, therefore, seems likely that the middle ear of echolocators is not specifically adapted to transduce a certain range of frequencies better than that of non-echolocators. However, middle ears of different species may still differ in the absolute minimum power (Sound Pressure Level, SPL) that can be detected. We hypothesise that the minimum threshold pressure level of echolocators should be lower than of non-echolocators. Such a higher sensitivity could be accomplished by the receptor organ or by the middle ear. It is likely that echolocating Swiftlets in their noisy colony would also benefit from a higher than average signal to noise ratio compared to non-echolocators, which can be accomplished by the central nervous system, and is thus an adaptation in signal processing. This can, however, only be realized provided the signal is detected, which is a particular concern in echolocation. The sound pressure level of an echo is relatively low, since the echo has travelled twice the distance of the bird to the reflecting object, which considerably attenuates the signal. This is especially true for higher frequencies, which are more effectively attenuated than lower frequencies, but are also more informative in echolocation, because lower frequencies of an echo are more easily masked by those of background noise. In addition, the SPL of the returning echo is also considerably decreased by spreading loss of energy from the source, both the echolocating bird and the reflecting surface. This spreading loss is high even at short

distances. Directionality of the echo click could decrease the spreading loss, but the sound-reflecting surface will reflect the click in all possible directions. The middle ear should therefore be able to detect and transduce the high-frequency, low pressure sounds of the echo. To accomplish this, the middle ear of echolocators may be morphologically adapted to be a better transducer, i.e. detect sounds of lower pressure levels and transduce these low SPL sounds sufficiently well for detection by the inner ear.

Lower minimum detection levels could be accomplished in the middle ear by (1) at the input side higher sensitivity of the middle ear itself to incoming sounds, e.g., through lower masses of the middle ear structures, and (2) at the output side larger oscillation amplitudes of the footplate at the oval window in the cochlea – through changes in the configuration of the ossicular chain – so that the cochlea could detect oscillations more easily.

A higher output-amplitude can only be realized if the most important function of the middle ear – bridging the impedance difference between air and the cochlea (e.g., Saunders et al., 2000) – is not adversely affected. In impedance matching, low pressure sound waves in air must be transformed into high pressure waves in the cochlear fluid. This is accomplished by two systems: (1) the tympanum to footplate area ratio and (2) the lever system (Fig. 1a and b). A large tympanum combined with the small columellar footplate results in a pressure gain at the oval window. The extracolumella attaches to the tympanum by means of three processes. The names of these processes are confusing in the literature. Pohlman (1921) referred to them as the extra-, superior-, and inferior-stapedial processes. Gaudin (1968) referred to the same processes as the extra, supra, and inferior columella, and Kühne and Lewis (1985) as the rostral, caudal, and ventral processes. We adapt the latter nomenclature in this paper. The lever system (e.g., Gaudin, 1968; Norberg, 1978) (Fig. 1a and b) is defined as the Force Lever (FL) and Resistance Lever (RL). The force lever is identified as the line that runs from the tip of the rostral process to where it crosses the line between the tips of the ventral and caudal processes (VP–CP) perpendicularly (Fig. 1). The resistance lever is the line running from the scapus–extracolumella connection perpendicular on VP–CP. The lever ratio (FL:RL) is proportional to the output force, and the impedance is the ratio of that force and the velocity of the footplate. However, the lever ratio is inversely proportional to the displacement of the RL. The amplitude of the oscillation of the columella decreases when the lever ratio increases. Thus, modification of the lever arms in order to increase output-amplitude will result in a decrease in impedance matching performance and the other way around. Decreased impedance matching performance of the lever system can however be compensated by an increase in the area ratio of tympanum and oval window. The middle ear, and more particularly the lever system of the extracolumella and columella, could thus be modified to gain a

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