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SENSORY BIOLOGY

Bats united by cochlear development

Bat species that echolocate using signals from their larynx, and those that do not, all share a similar pattern of inner ear development that is distinct from other mammals, implying a single evolutionary origin of laryngeal echolocation.

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Flight defines bats, a single lineage of mammals[1]. Most bats today echolocate using biosonar signals produced in the larynx, while a few species of pteropodid bats echolocate with tongue clicks[1]. Whether laryngeal echolocation evolved once and was then lost in pteropodids, or evolved multiple times after bats' early radiation is an evolutionary mystery[2]. Writing in *Nature Ecology & Evolution*, Zhe Wang and colleagues[3] demonstrate that the cochleae of fetal stage embryos of both sorts of bats are strikingly similar to one another and unlike those of fetal stage embryos from other groups of non-echolocating mammals. This new approach supports the view that laryngeal echolocation originated once in bats. Evolutionary biologists have long been interested in the origin and evolution of bats, especially in the wake of changes in the superfamilial classification of bats[4]. This original study sheds new light on the topic.

Cochleae — bones that house the inner ears — may be fundamental to and indicative of echolocation in bats and toothed whales[5]. For echolocators, larger and more coiled cochleae mean greater sensitivity to higher frequency signals, as well as better frequency discrimination[6]. Adult cochlear morphology varies markedly in bats, differing most between bats capable of laryngeal echolocation and those that are not (Fig. 1). Although there is considerable diversity in adult cochlear structure among laryngeally echolocating bats, the cochleae are consistently large and prominent. Conversely, the cochleae of adult pteropodids are relatively small and less varied, essentially like those of other non-echolocating mammals[3].

These differences in adult form within bats appear to support the idea that pteropodids never had capacity for laryngeal echolocation. By considering fetal cochlear development, Wang *et al.* have turned the argument on its ear. They report an early pattern of rapid cochlear development across bats, while the cochleae of the other mammals they considered start to develop much later. At later stages of development, the growth trajectory continues unabated in laryngeal echolocating species but slows in pteropodids. Early cochlear development in bats is thus distinctly different from that of non-echolocating mammals; suggesting pteropodids once had a capacity for laryngeal echolocation that was subsequently lost in this lineage.

The cochleae of one of the first known fossil bats (*Onychonycteris finneyi*[2]; Fig. 1) are smaller than those of other fossil bats and living laryngeal echolocating bats. This feature has been used to support the view that *O. finneyi* did not echolocate[7]. However, the handful of pteropodids, terrestrial mammals and cave-dwelling birds that echolocate with clicks also have relatively less developed cochleae as adults. For some of these species and in some blind humans[8], echolocation is less sophisticated and facultative. For example, birds, including echolocating species, have much lower sensitivity to high frequency sounds than the vast majority of mammals, echolocators or not. In light of this, the study of Wang *et al.* provides still more support for the idea that the common ancestor of all bats had the capacity for echolocation.

We agree that the common ancestor of bats could echolocate, but perhaps not with laryngeal echolocation signals. Clicks, not calls, are the rule rather than the exception among echolocators and do not demand the specializations we observe in the larynges of most modern day echolocating bats. Differences in echolocation call design and laryngeal structure among echolocating lineages indicate that, after its origin, call design and behaviour continued to diversify. Examples of its diversification in bats include the use of terminal (feeding) buzzes by most (but not all) bats that hunt flying insects, as well as the development of derived high duty cycle echolocation in two distinct lineages of bats[9]. High duty echolocators separate pulse and echo in frequency, whereas all of the other known echolocators separate them in time.

Wang and colleagues do not directly address theories about the role of flight and echolocation in the origin and diversification of bats[10]. Did echolocation evolve before or after flight? Or did flight

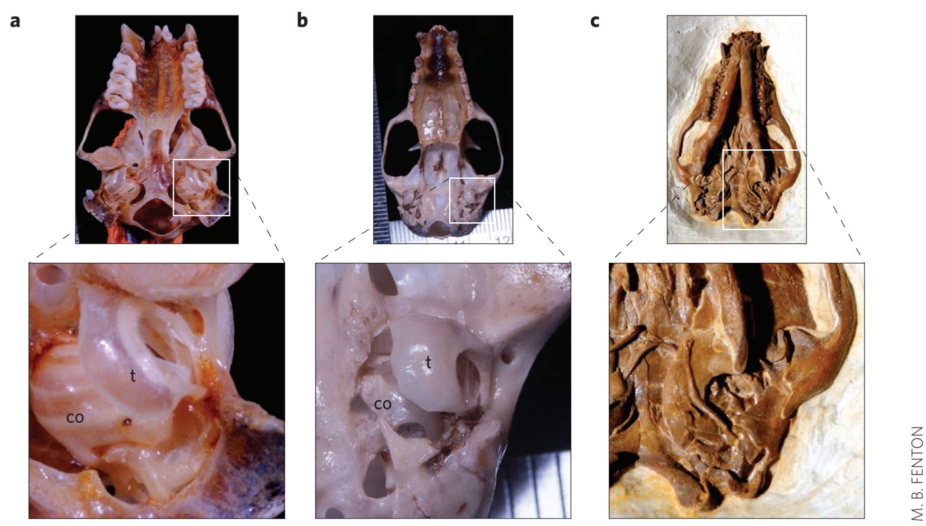

Figure 1 | Cochlear regions of bat skulls. **a**–**c**, Ventral views of skulls showing the cochlear region (insets) of a laryngeally echolocating bat (**a**, *Noctilio leporinus*), a non-echolocating pteropodid (**b**, *Epomops franqueti*) and the oldest known fossil (**c**, *Onychonycteris finneyi*). The tympanic bone (t) partly covers the cochlea (co) in **a** and **b**. The cochlea is not obvious in **c**.

and echolocation evolve in tandem? We suggest that rapid initial development of cochleae across bats and the relatively small cochleae in the most ancient fossil bat support tandem development of these two key innovations that describe most, but not all, of today's bats. ❐

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