Veselka et al. *reply*

Replying to: U. Wittrock *Nature* **466,** doi:10.1038/nature09156 (2010)

Wittrock suggests that a stylohyal–tympanic connection in laryngeally echolocating bats as the one described in our study[1] could transmit laryngeal vibrations to both ears[2]. This could represent a 'local oscillator', forming part of a heterodyne-like detection system for precise target detection and localization. The essence of this exciting idea is that the externally transmitted echo (signal of interest) received by the ears would be mixed (multiplied) with an internally transmitted copy of the outgoing biosonar sound (reference signal) via vibrations of the stylohyal. The multiplicative mixing would generate two new signals—one at the sum and the other at the difference of the original inputs—and after low-pass filtering the remaining components would include a difference frequency signal that varied in its rate of amplitude modulation (AM).

Wittrock's proposal is a logical extension of the first function that we suggested for the stylohyal–tympanic connection in bats[1]. A heterodyne-like mechanism may be possible because AM rates up to a few kilohertz could be encoded in the responses of primary auditory afferent neurons. This mechanism applies most obviously to high duty cycle echolocating bats—species that regularly exploit Doppler-shifted echoes (for example Rhinolophidae, Hipposideridae, *Pteronotus parnellii*)—but its use is not precluded in low duty cycle bats that emit calls containing more than a single (narrowband) frequency. Indeed, a heterodyning mechanism may help to explain why so many bats emit downward hyperbolic frequency-modulated (FM) sweeps. In these signals, such linear period modulated chirps emphasize (elongate) the duration of the lowest frequencies in the FM sweep.

One difficulty with the heterodyning hypothesis lies in identifying the nonlinear biological mechanism for multiplying bone-conducted vibrations with airborne-conducted vibrations. Another potential difficulty is the difference in velocity between the speed of sound in bone ($\sim$3,500 m s^{-1}) and the speed of sound in air ($\sim$344 m s^{-1}), which could result in a latency difference at the cochlea. For the stylohyal–tympanic bony connection to function as part of a heterodyning system, either (1) there is a mechanism to delay vibrations transmitted along the hyoid apparatus, and/or (2) the tympanic must continue to 'ring' after the outgoing biosonar vocalization has ended so that the signal can be mixed with later returning echoes. Intervening elastic elements within the hyoid chain may generate the delay necessary for possibility (1) but could also introduce significant damping of bone-conducted vibrations. Possibilities (1) and (2) remain to be investigated experimentally, but clearly represent productive areas for future research.

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1. Veselka, N. *et al.* A bony connection signals laryngeal echolocation in bats. *Nature* **463**, 939–942 (2010).
2. Wittrock, U. Laryngeally echolocating bats. *Nature* **466,** doi:10.1038/nature09156 (2010).

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