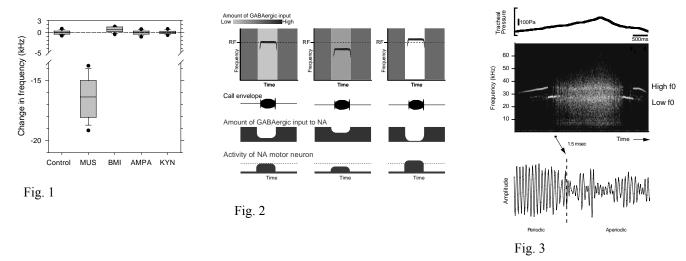
Why listen to bats ? - How hearing affects voice in a mammal

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Abstract Hearing one's own voice is essential for the production of correct vocalization patterns in many birds and mammals, including humans. Echolocating bats, in particular, adjust temporal, spectral and intensity parameters of their echolocation calls by precisely monitoring the characteristics of the returning echo signals. However, neuronal substrates and mechanisms for auditory feedback control of vocalizations are still largely unknown in any vertebrate. Horseshoe bats, above all, represent a valuable experimental model system to finally tackle this problem. They compensate even for subtle frequency shifts in the echo caused by flight-induced Doppler-effects by precisely adjusting not only spectral (call frequency) characteristics of their echolocation calls but, as we recently determined, also their temporal attributes (call duration, call rate). This "Doppler-shift compensation (DSC) behavior" therefore provides the unique opportunity to dissect the neural basis for auditory feedback control of key parameters of mammalian vocalizations, i.e., their frequency and their timing.

Previously (Fig. 1), we determined how frequency, duration, and interpulse interval of bat echolocation pulses were affected by changes in the synaptic activity within the vocal motor nucleus, nucleus ambiguus (NA) by injecting various excitatory and inhibitory transmitter agonists and antagonists into the NA of horseshoe bats. We showed that changes in the synaptic activity within the NA affect different sets of larvngeal motoneurons that vield changes in different call parameters. Our results predicted a specific activity pattern in cricothyroid motoneurons, which control call frequency (Fig. 2): lower frequencies are not caused by a reduction in excitatory input to these motoneurons. Instead, they possess an intrinsic spontaneous activity, which is independent of glutamatergic synaptic input and only modulated by GABAA. When not calling, this spontaneous activity is constantly suppressed by GABAergic input from premotor structures. During call emission, premotor input releases this inhibition, and the amount of release from inhibition is indirectly proportional to call frequency. One aspect of the study presented here was aimed at testing this model. For this purpose, we recorded single unit activity from the NA and simultaneously injected various transmitter agonists and antagonists in spontaneously echolocating horseshoe bats while they adjusted call parameters in response to electronically altered auditory feedback signals of their own calls. Indeed, we found evidence for the presence of such inhibitory (inter)neurons in NA. Another project aimed at quantifying the biomechanical properties of the bat larynx. tracheal air flow resulted in two distinct frequency bands that are non-harmonically related (Fig. 3; high F_0 : echolocation pulses; low F_0 : communication signals), and changes in air pressure revealed transitions from periodic to chaotic that occurred within a single cycle ($\leq 20 \mu s$).



Keywords Rhinolophus, horseshoe bat, Doppler-shift compensation, audio-vocal feedback, non-linear dynamics