Audiovocal interactions during development?
Vocalisation in deafened young horseshoe bats vs.
audition in vocalisation-impaired bats

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Summary. Horseshoe bats (Rhinolophus rouxi) were deafened in their 3rd–5th postnatal week. Subsequently their vocalisations were monitored to evaluate the impact of audition on the development of echolocation pulses. Hearing impairment affected the echolocation pulses as follows: the frequency of the constant frequency (CF) component was altered by between +4 kHz and −14 kHz, and the dominance of the second harmonic of the pulses was neutralised by a relative increase in intensity of the first and third harmonics.

A second experiment focused on possible influences of acoustical self-stimulation with echolocation pulses on the establishment of auditory fovea representation in the inferior colliculus (IC). Frequency control of echolocation pulses was disrupted by larynx denervation. Thereafter, the bats produced multiharmonic echolocation signals (4–11 harmonics) varying in frequency. IC tonotopy, however, as monitored by stereotaxic electrophysiology, showed the same developmental dynamics as seen in control specimens (Fig. 10).

Both experiments indicate that throughout postnatal development echolocation pulses are under auditory feedback control, whereas maturation of the auditory fovea and shifts in its frequency tuning represent an innate process. The significance of this postnatal development might be the adjustment of the vocal motor system of each bat to the frequency of its 'personal' auditory fovea.

Key words: Ontogeny – Audition – Vocalisation – Sensorimotor interaction – Rhinolophus rouxi

Introduction
In horseshoe bats the frequency of echolocation pulses is controlled by an auditory feedback system (Schnitzler 1968; Schuller et al. 1974, 1975). Typical echolocation pulses consist of brief 1- to 2-ms initial frequency modulations (FM) towards higher frequencies, followed by 20- to 50-ms-long constant frequency components (CF). The pulses are terminated by brief downward-sweeping FMs. Resting bats emit echolocation pulses with pure tone components closely matched to a narrow frequency band which is vastly over-represented in the bats' auditory system (Schuller and Pollak 1979). During flight the bats vary the frequency of the emitted pulses in order to keep the frequency of the reflected echo within this over-represented frequency range (Schnitzler 1968). The set-point of this feedback control system, termed the 'reference frequency' (Schuller et al. 1974), can vary in different specimens by about 10 kHz (Rhinolophus rouxi: Vater et al. 1985). However, this reference frequency is constant for each individual bat and is always related to the tuning of identical areas within central auditory nuclei (Rübsamen et al. 1988a, b). In the inferior colliculus (IC) the corresponding site, located ventromedially, is named 'central representation of the auditory fovea' (Rübsamen and Schäfer 1990, companion paper). This term was adopted from the visual system and designates the enormous over-representation of a narrow, behaviourally relevant frequency range. The tuning of the auditory fovea is individually specific within sexual dimorphic ranges, i.e., adult male horseshoe bats have foveal frequencies within the range of 70–75 kHz and females 74–79 kHz (Rübsamen et al. 1988b).

During the ontogenesis of Rhinolophus rouxi, frequency representation in the central auditory system passes through maturational changes, one of which is the alteration of the frequency-place code within the audito-
ry fovea (Rübsamen and Schäfer 1990, companion paper). In young bats the auditory fovea is initially tuned to a frequency range of 60–68 kHz, and from the 3rd to the 5th week the foveal frequencies progressively increase up to the adult values.

Observation of vocal development shows that the bats only start to produce echolocation pulses when the central representation of the auditory fovea has been established. Right from the beginning, the frequencies of the echolocation pulses coincide with the foveal frequencies, and during subsequent development both pass through parallel increases (Rübsamen 1987).

To study the audiovocal co-development during maturation of the echolocation system two hypotheses were considered. The first is called the auditory dominance hypothesis. It states that the (genetically determined) development of the auditory system is essential for the maturation of the echolocation system. It further suggests that in young bats, too, the echolocation pulse frequency is controlled by auditory sensation, i.e., that young bats utilise the same auditory feedback control of vocalisation as adults. Thus, the bats would only start to produce ‘regular’ echolocation signals as the auditory fovea becomes established. In each individual the pulse frequency would be adjusted to the frequencies represented in its individual auditory fovea. During maturation, the foveal tuning would alter and, consequently, in each single bat the vocalised frequencies would pass through the entire range of the shifting foveal frequencies.

The second hypothesis is called the vocal dominance hypothesis. This suggests that, during development, the establishment of foveal representation in central auditory nuclei in each individual bat is coupled to the perception of the bat’s own pulse frequencies. It postulates that in young bats the immature appearance of the echolocation pulses is due to immature development of the larynx. The frequency increase observed during postnatal development would then be a consequence of the maturation of the pulse-producing organ, the larynx. Following this supposition, the neuronal responsiveness in central auditory nuclei would be modified by the sensory input given by the acoustical self-stimulation. As a consequence, the ‘central representation of the auditory fovea’, characterised as a population of neurons with increased sensitivity, would first emerge when the bats start to produce echolocation pulses, and the foveal tuning would match the frequencies of the echolocation pulses. During further development the foveal tuning would be shifted to higher frequencies in accordance with the increase in vocalised pulse frequency. Finally, in the adult specimen this high sensitivity of unit responsiveness in central auditory nuclei would become ‘stabilised’ as the bat’s individual-specific central representation of the auditory fovea.

In the present investigation two experiments were performed to test the validity of each of the two hypotheses (Fig. 1).

1. Young bats were deafened and the vocalisations emitted after recovery from surgery were compared to the presurgical standard. If deafening had no effect on echolocation pulse frequency, this would show that pulse production in young bats is independent of auditory feedback control. This result would support the vocal dominance hypothesis. Alternatively, any postsurgical change in the design of vocal pulses would show that auditory feedback control existed and support the auditory dominance hypothesis.

2. In a second group of young bats, the frequency control of echolocation pulses was disrupted by partial denervation of the larynx. The subsequent development of central auditory frequency maps, including the tuning of the auditory fovea, was monitored in these experimental animals and compared with the development found in control bats. If these lesions caused developmental effects on neural responsiveness in central auditory nuclei, and especially at the representation sites of the auditory fovea, the vocal dominance thesis would be supported. On the other hand, this hypothesis would be rejected and the auditory dominance hypothesis supported if the development of foveal tuning in bats with aberrant vocalisations proved to be the same as in control bats.

Since each of the above experiments would give evidence for or against the validity of both the development hypotheses, comparison of the results of both experiments might clarify whether the development of the echolocation system in rufous horseshoe bats is controlled by the auditory system or by the vocalisation system.

Materials and methods

The experiments were performed in a field station in Sri Lanka next to a large maternity colony of rufous horseshoe bats (Rhinolophus rouxi). The investigation took place during the maternal lactating period, lasting from October to November 1987. A sample of 23 young bats was taken from the cave in their 3rd–4th postnatal week. This is the critical period for the development of the auditory fovea in young horseshoe bats (Rübsamen and Schäfer 1990, companion paper). The bats were reared separately from their mothers in an