A modeling approach to explain pulse design in bats

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Abstract In this modeling study we wanted to find out why bats of the family Vespertilionidae (and probably also members of other families of bats) use pulses with a certain bandwidth and duration. Previous studies have only speculated on the function of bandwidth and pulse duration in bat echolocation or addressed this problem by assuming that bats optimize echolocation parameters to achieve very fine acuities in receiving single echoes. Here, we take a different approach by assuming that bats in nature rarely receive single echoes from each pulse emission, but rather many highly overlapping echoes. Some echolocation tasks require individual echoes to be separated to reconstruct reflection points in space. We used an established hearing model to investigate how the parameters bandwidth and pulse duration influence the separation of overlapping echoes. Our findings corroborate the following previously unknown or unsubstantiated facts:

(1) Broadening the bandwidth improves the bat’s lower resolution limit.
(2) Increasing the sweep rate (defined by bandwidth and pulse duration) improves acuity of each extracted echo.
(3) Decreasing the sweep rate improves the probability of frequency channels being activated.

Since facts 2 and 3 affect sweep rate in an opposing fashion, an optimum sweep rate will exist, depending on the quality of the returning echoes and the requirements of the bat to improve acuity. The existence of an optimal sweep rate explains why bats are likely to use certain combinations of bandwidth and pulse duration to obtain such sweep rates.

1 Introduction

In this paper we attempt to find out what the function of bandwidth and pulse duration is in bat species that use broadband echolocation calls, such as vespertilionid bats. A broad bandwidth, in the past, has been viewed as an adaptation of bats to increase acuity, which is the case for a fully coherent receiver (Simmons and Stein 1980) and probably for a wide range of receiver models (Sanderson et al. 2003). In reviews, bandwidth is often considered an adaptation mainly to improve target localization (e.g., Schnitzler and Kalko 2001; Schnitzler et al. 2003; Simmons et al. 2004). Reducing pulse duration is regarded as an adaptation to improve the separation of echoes in target classification tasks (Schnitzler and Kalko 2001; Schnitzler et al. 2003; Denzinger et al. 2004). The descriptions of the possible function of bandwidth and pulse duration found in reviews are based partly on logic, previous modeling studies, and echolocation behavior of bats in the field. Only in one recent study a systematic approach was taken to investigate the function of bandwidth and pulse duration (Holderied et al. 2006). Two psychophysical studies on Eptesicus fuscus confirmed that decreased bandwidth deteriorates acuity (Surlykke 1992; Simmons et al. 2004). In this paper we do not want to contradict the fact that bandwidth can improve acuity and that short pulse durations are beneficial in classification tasks. However we do challenge the view that bats evolved bandwidths of several octaves to localize a single target very accurately. Most natural targets do not give rise to single echoes, but to many highly overlapping echoes.
Analyzing such sets of highly overlapping echoes appears a far more natural task than trying to pinpoint one single echo. A narrow bandwidth already suffices to achieve an acuity in the microsecond range, to this aim a multi-octave bandwidth therefore seems redundant.

In this study, we therefore hypothesize that bats evolved important pulse parameters, such as bandwidth and duration, with the aim of optimizing the separation of the many overlapping echoes that return to the bat’s ear after each pulse emission. The results of previous experiments on two-echo resolution (Simmons 1993; Simmons et al. 1998) indicate that broadcast bandwidth should be high in order for the auditory system to find as many frequency notches and peaks as possible (Saillant et al. 1993). To investigate the effect of signal bandwidth and pulse duration on the ability to resolve a returning set of echoes, we used a hearing model that was designed to mimic the mammalian hearing system, modified to work in the ultrasonic range. In this paper we provide a biological motivation for each processing stage of the model, and show that it is parsimonious, also working for inputs differing strongly from our standard test input. Although our hearing model makes use of information over a broad spectral range, it differs from previous models by initially only extracting echoes in the temporal domain. We thoroughly discuss differences between our model and other existing hearing models.

We also present an overview of acuities and resolutions measured in real bats to show that our model yields a better acuity than most behavioral experiments show, but a comparable resolution.

When a bat resolves a series of echoes, it will probably be interested in obtaining not only the correct number of echoes, but also their temporal occurrence with the best possible acuity. We therefore wanted to know to what sensory purpose a broad bandwidth is more important: to perceive the correct number of echoes, or to locate each of the overlapping echoes very precisely in time.

Our results suggest that perceiving the correct number of echoes is the more demanding task with regard to bandwidth, whereas sweep rate strongly limits the acuity in temporally resolving individual echoes of a series. Our data also show the penalty incurred by using extremely high sweep rates, clarifying why certain values of pulse parameters are likely to be used by bats in the field.

2 Methods

2.1 Bat hearing model (Fig 1)

All simulations performed for this paper were conducted using Matlab 6.5, release 13 (The Mathworks Inc, Natick, Massachusetts). The bat hearing model was the same as that described in Weißenbacher and Wiegrebe (2003), which is a 60-channel gamma-tone filterbank with filter bandwidths derived from suppression tuning curves (Weißenbacher et al. 2002). The gamma-tone filterbank is a constant Q filterbank, typical of a nonspecialized mammalian cochlea (Kössl 1992; Weißenbacher et al. 2002; Wittekindt et al. 2005).

Many neurobiological handbooks devote a section to the highly specialized Doppler sonar system with a cochlea which is tuned sharply around one specific frequency. The hearing model used in this paper, however, is based on a general nonspecialized mammalian cochlea, probably typical of >80% of all species of echolocating bats.

![Fig. 1](image_url)