Time Domain Echo Analysis in the Bat
Phyllostomus discolor

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Contents

Zusammenfassung

Die beeindruckende Fähigkeit von Fledermäusen, sich mit Hilfe der Echoortung nicht nur zu orientieren sondern auch geortete Objekte klassifizieren zu können, wirft in manchen Aspekten immer noch Fragen auf. Von besonderem Interesse ist dabei, welche Art von Informationen die Fledermäuse aus dem aufgefangenen Echo entnehmen können, und wie sie dies bewerkstelligen.

Diese Dissertation beschreibt drei unterschiedliche Herangehensweisen an die Untersuchung der unterschiedlichen Informationen, die im Zeitbereich eines Echos vorhanden sind. Das erste Kapitel befasst sich mit den äußerst komplexen Echos, die Fledermäuse in ihrer natürlichen Umgebung von großen Objekten wie z.B. Bäumen erhalten. Diese Echos können nicht unter Ausnutzung ihres Frequenzgehalts bewertet werden, sondern nur durch statistische Auswertung ihrer zeitlichen Information. Im vorliegenden Fall ist der Grad der Einhüllendenfluktuation des Echos gemeint, der auch als Echorauhigkeit bezeichnet werden kann. In einem Rückspielexperiment mit virtuellen Objekten unter Anwendung eines 2-AFC-Paradigmas (two alternative, forced choice) wurde die Empfindlichkeit der Fledermaus *Phyllostomus discolor* bezüglich der Echorauhigkeit bestimmt, indem wir untersucht haben wie gut die Fledermaus zwei Echos mit unterschiedlicher Rauhigkeit unterscheiden kann. Dies wurde durch Erzeugung künstlicher akustischer Abbilder mit unterschiedlicher, vorher festgelegter Rauhigkeit und chaotischem Frequenzbereich erreicht. Durch Faltung zweier dieser akustischen Abbilder mit einem aufgezeichnetem Ortungslaut der Fledermaus konnten Phantom-Echos von virtuellen Objekten erzeugt und gleichzeitig zur Fledermaus zurückgespielt werden. Wir konnten zeigen, dass diese akustischen Abbilder eine Mindest-Rauhigkeit von 2.5 (quantifiziert als dekadischer Logarithmus des 4. Moments) sowie einen Mindest-Rauhigkeitsunterschied von 0.3 aufweisen müssen, um von der Fledermaus zuverlässig unterschieden werden zu können.

Zusammenfassung

Im zweiten Kapitel wurde dieses Experiment mit modifizierten akustischen Abbildern wiederholt. Die im ersten Kapitel verwendeten Abbilder (und damit auch die daraus entstehenden Echos) waren unmoduliert, was bedeuten würde dass der Ortungslaut der Fledermaus das beschallte Objekt (z.B. das Laubwerk eines Baums) komplett durchdringt. Neue Erkenntnisse zeigen aber, dass die Zeitsignale von Echos natürlicher Objekte im Allgemeinen entweder lauter oder leiser werden. Durch Anpassung der akustischen Abbilder aus dem ersten Kapitel untersuchten wir, welche Auswirkungen diese beiden Lautstärke-Veränderungen auf die Fähigkeit zur Rauhigkeitsunterscheidung bei der Fledermaus *P. discolor* haben. Laut unseren Ergebnissen sind diese Veränderungen aber ohne Folgen. Des Weiteren versuchten wir, die gemessenen Unterscheidungsschwellen mit den vorhandenen Daten über die Rauhigkeit der akustischen Abbilder einheimischer Bäume und Sträucher in ein Verhältnis zu setzen. Obwohl sich ein quantitativer Vergleich aus verschiedenen Gründen als sehr schwierig durchzuführen erwies, konnten wir in einem qualitativen Vergleich zeigen, dass die Rauhigkeitsunterscheidung, zu der *Phyllostomus discolor* in der Lage ist, ausreichend sein könnte um eine echoakustische Unterscheidung einheimischer Bäume vorzunehmen.

Das dritte Kapitel befasst sich mit einem anderen Aspekt des Zeitbereichs eines Echos. Ein äußerst wichtiges, jedoch bis heute nicht vollständig beantwortetes Thema bezüglich der Echoortung bei Fledermäusen betrifft die Frage, ob und zu welchem Ausmaß Fledermäuse in der Lage sind, das akustische Abbild eines georteten Objekts aus dessen Echo zu extrahieren. Voraussetzung dafür wäre eine präzise Analyse der Frequenz- und Zeitbereichs des Echos, mit anderen Worten des Magnituden- und Phasenspektrums. Bisherige Studien bestimmten die Phasensensitivität von Fledermäusen im Hinblick auf die Echoverzögerung. Dabei wurde eine Bestimmungsgenaugkeit im Nanosekunden-Bereich gemessen, was bedeuten würde dass die Fledermäuse vollständigen Zugriff auf das Phasenspektrum eines Echos haben. Unter Verwendung einer anderen Methode haben wir die Phasensensitivität von *P. discolor* im Hinblick auf die Echodauer gemessen. Unsere Ergebnisse zeigten eine Sensitivität bezüglich der Echodauer, die im Mikrosekundenbereich liegt und damit mehrere Größenordnungen niedriger ist als die für Echoverzögerung. Dies lässt vermuten, dass verschiedene Aspekte der zeitlichen Echoinformation, wie Verzögerung oder Dauer, auf unterschiedlichen Wegen mit unterschiedlicher Empfindlichkeit verarbeitet wer-

den. Entsprechend kann die Behauptung einer perfekten Phasensensitivität nicht mehr aufrechterhalten werden.

Die Ergebnisse, die in dieser Dissertation vorgestellt werden, erbringen damit neue Erkenntnisse bezüglich dem im Zeitbereich eines Echos vorhandenen Informationsgehalt und dem Zugang, den eine Fledermaus darauf hat.

Zusammenfassung

Summary

The outstanding ability of bats to use their sense of echolocation for orientation and object classification still remains a mystery in some aspects. Of special interest is the question about what kind of information the bats extract from the perceived echo, and how this extraction is achieved.

This thesis describes three different approaches to investigate the different aspects of the information content available in an echo's time domain. The first chapter addresses the fact that bats have to deal with very complex object echoes in their natural habitat, which cannot be classified by exploitation of their frequency content but solely through statistical evaluation of their time domain properties, in this case the degree of the echo's envelope fluctuation or roughness. In a virtual object playback experiment using a two-alternative, forced choice paradigm, we investigated the sensitivity of the bat *Phyllostomus discolor* in respect to echo roughness by determining its performance in discriminating two echoes with differing roughness. This was achieved by generating artificial acoustic images with different predefined roughnesses and a chaotic frequency domain. Through convolution of two of these acoustic images with a recorded echolocation call of the bat, phantom echoes of virtual targets can be created and played back to the bat simultaneously. We discovered that the acoustic images must possess both a defined minimum roughness of 2.5 (quantified as the base-10 logarithm of the 4th moment) and a minimum roughness difference of 0.3 to be successfully discriminated by the bat.

In the second chapter, this experiment is repeated with modified acoustic images. The acoustic images (and therefore the resulting echoes) used in the first chapter were unmodulated, suggesting a complete acoustic permeation of the bat's call through the ensonified object. New data shows that the waveforms of echoes from natural complex objects often feature an amplification or an attenuation over time. Through accordant modification of the acoustic images used in the first chapter, we examined which impacts these two modification types have on the roughness-discrimination of *Phyl-*

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lostomus discolor. Our data shows that the discrimination performance is not affected regardless of the modification type. We also tried to compare our discovered discrimination thresholds with available data for the roughness of acoustic images of natural objects. Although a quantitative comparison turned out to be difficult for various reasons, a qualitative comparison showed that the roughness discriminating performance of *Phyllostomus discolor* could be sufficient to allow echo-acoustic discrimination of natural objects by their acoustic roughness.

The third chapter concerns a different aspect of an echo's time domain. A crucial, not yet fully answered question about bat sonar is if, and to what extent, bats are able to extract the acoustic image of an ensonified object out of the echo. Prerequisite for this is an accurate analysis of both frequency and time information, in other words of the echo's magnitude and phase spectra. Previous studies measured the phase sensitivity of bats in terms of echo delay and found a temporal acuity in the nanosecond-range, suggesting perfect access to the echo's phase. Using a different approach, we measured the phase sensitivity of *Phyllostomus discolor* in terms of echo duration. Our results showed a phase sensitivity in terms of echo duration that is in the microsecond range and therefore by several orders of magnitude lower than the reported sensitivity for echo delay. This suggests that different aspects of temporal echo information, like delay or duration, are processed in different ways with different sensitivities. Correspondingly, the claim of overall, perfect phase sensitivity as such cannot be maintained.

The findings presented in this thesis contribute new insights into the information content that is available in an echo's time domain, and into the magnitude of the bats' access to this content.

Introduction

The multitude of perceptual modalities that is utilized by every living being to gather information about or interact with the environment is truly astounding. Be it visual, acoustic, olfactory, tactile, taste or electroreception - there seems to be no end to nature's creativity. Depending on a creature's habitat and way of life, there's usually at least one modality which is especially suitable and therefore enhanced, like the star-nosed mull's (*Condylura cristata*) sense of touch, a cat's ability to see in almost complete darkness or the astounding ability of migrating birds to orient by the earth's magnetic field.

Among those many remarkable perceptual abilities that are known to us, the sense of echolocation is doubtless one of the most fascinating. Echolocation describes the ensonification of an object with an usually ultrasonic acoustic signal. The signal is then reflected by the object and changes in the process, depending on the appearance of the object. By evaluating the changes in the echo and the delay between signal emission and echo arrival, information e.g. about the object's distance or size can be acquired (Simmons, 1971; Simmons & Vernon, 1971). For humans, who usually rely heavily on their sense of sight, it remains very difficult to grasp how our world must 'look' when perceived solely in an acoustical manner. There are blind humans who are to a certain extent able to use acoustical cues (even their own tongue-clicks), thereby achieving a sort of low-level echolocation giving them a basic impression of their surroundings. Still, acting and orienting based solely on this modality remains explicitly restraining for us.

Although there are several animal species who use echolocation, like the cave swiftlets of the family *Apodidae*, some tenrec species (e.g. *Echinops telfairii* (Gould, 1965)) and some shrew genera (*Sorex* and *Blarina*), the true known masters of this ability are found in the tooth-whale species and, especially, among the echolocating bats.

Echolocation allows bats to orient and navigate seemingly effortlessly in even the most difficult surroundings in complete darkness. Using echolocation, bats can not only pinpoint the exact location of any given object in space, it also enables them to gather infor-

mation about the size, the surface composition and the three-dimensional structure of the object (Habersetzer & Vogler, 1983; Neuweiler, 1989; Schmidt, 1988, 1992; Schmidt et al., 2000; Simmons et al., 1974).

All this information is encoded as the object's acoustic image within the echo. The acoustic image of an object is the sum of the reflections in response to an acoustic impulse of theoretically infinite shortness and infinite amplitude (Dirac impulse); it is called the object's impulse response (IR) (see figure 0.1, upper panel). Although also being rather short and spectrally wide-banded, a typical echolocation call can't be compared to an impulse. The echolocation call of the bat *Phyllostomus discolor* for example is several milliseconds long and only covers a certain frequency range (45-90 kHz), the resulting echo is therefore not the IR itself, but the IR imprinted on the echolocation call (see figure 0.1, lower panel).

A further consequence of this is that the echolocation call sort of "blurs" the IR, which makes the echo longer and hence more difficult to evaluate the embedded IR. It would therefore be an advantage for bats to be able to extract the IR out of the echo, which would allow the bat to have full access to the original information. Mathematically, this kind of extraction would be possible for instance by means of a cross-correlation of echolocation call and echo, who are both available to the bat.

There have been some indications that the bat *Eptesicus fuscus* is able to extract and evaluate spectral cues out of an echo (Simmons et al., 1974), and possibly uses these spectral cues together with temporal cues to obtain a specific acoustic image of the ensonified object (Simmons et al., 1990b).

Weissenbacher & Wiegrebe (2003) demonstrated that the bat *Megaderma lyra* indeed is able to acquire an ensonified object's acoustic image. For small virtual objects with a size of less than 3.4 cm, the bat *Megaderma lyra* was able to obtain a detailed internal representation of the object's acoustic image, in other words, its IR. For objects with this size, the echo information in the auditory periphery is coded predominantly in the frequency domain, as the IR duration of small objects like these (< 200 μs) is in the range of the temporal integration window of the auditory system of the bat (around 200 μs, (Weissenbacher et al., 2002)). Due to this, the individual amplitude peaks are not resolved separately in the auditory system, but merge into a single one. Thus, the temporal information contained in the echo is lost and the bats seem to evaluate the resulting specific spectral interference pattern. Simulations showed that a replication of the bats' performance was only possible, when based on the evaluation of the actual IR,
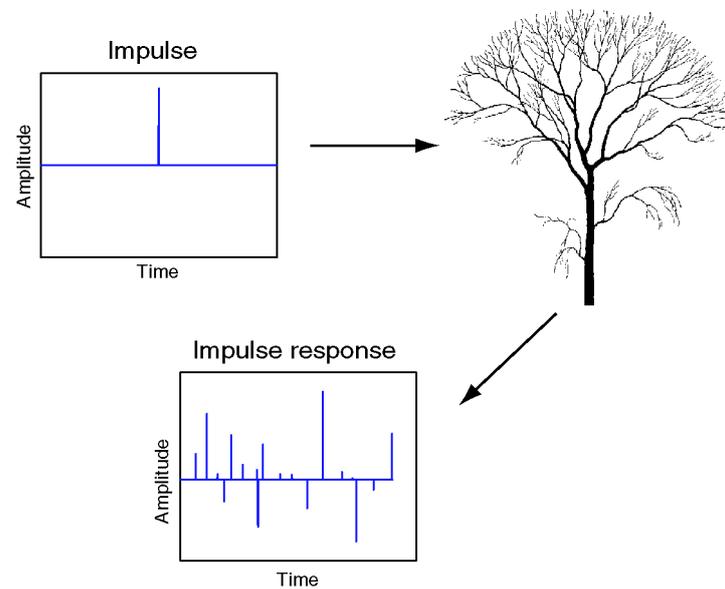
(a) Formation of an impulse response
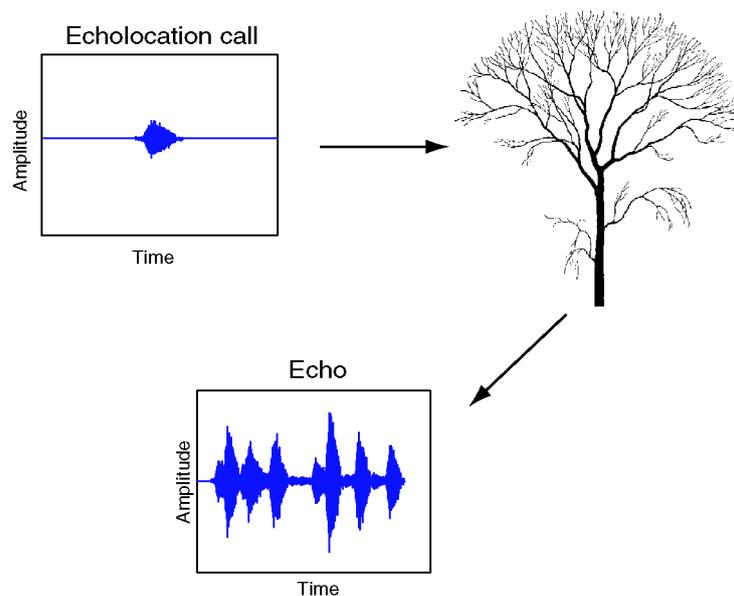
(b) Formation of an echo

Figure 0.1: a) Formation of an impulse response. A dirac impulse impinges on an object like a tree and is reflected by every surface of the object that is facing the source of the impulse. The distance between the individual surfaces defines the length of the temporal gaps between the reflections. b) Formation of an echo of the same object. In this case, the echolocation call of the bat is imprinted on the ensonified object's impulse response.

the echo itself was not sufficient. Interestingly, it seems like the bats continued to use this spectral evaluation strategy for a virtual object size up to 6.6 cm (corresponding to an IR duration of 390 μs), although now temporal information should also be available to them.

Still, the results of Weissenbacher imply that for all objects that are larger than 3.4 cm, or don't feature a stable spectral interference pattern because of changing IRs, evaluation of the interference pattern is not possible or expedient.

This is especially true for large natural objects like trees or bushes, which not only feature comparatively longer IR durations in the millisecond range, but also consist of a very complex structure with thousands of reflective surfaces which are provided by the leaves and branches. Moreover, this structure (and thus its IR) will be highly unstable over time because movements of the leaves due to wind will occur and a bat will rarely encounter a tree twice from exactly the same angle. Even if this should be the case, there would still be the problem that echoes reflected from these complex objects will have no systematic spectral interference pattern for the bat to evaluate.

Yet, it is reasonable that a bat should somehow be able to identify natural objects in order to navigate within complex surroundings or, in the case of frugivorous bats, for the classification of trees which provide food.

Müller & Kuc (2000) conducted a comparative analysis of the IRs of two different trees, namely one with only few but large, broad leaves (the weeping fig, *Ficus benjamini*) and a second one with many small and needlelike leaves (the spreading yew, *Taxus media*). They ensonified both from several hundred directions using a 60 μs pulse with a frequency range between 30 and 100 kHz, resembling the frequency range of a bat echolocation call. Indeed, they found a possible acoustical cue in the time domain of the echo. As every twig and every leaf ensonified by this pulse represents a reflecting surface, the shape of the resulting IR depends solely on the characteristics of these surfaces. The few but large and broad leaves of the weeping fig produce an IR with equally few reflections, which will have a rather high amplitude due to the leaves' size. The many small needlelike leaves of the spreading yew on the other hand result in an IR with many reflections, each of them having a small amplitude (see figure 0.2). In other words, the extent in which a IR's envelope fluctuates depends on the foliage type and -density. This envelope fluctuation can also be described as an IR's roughness.

The results of their analysis indicated that this IR roughness is a good predictor for the correct association of the IRs to the corresponding tree. A broad-leafed tree with few but
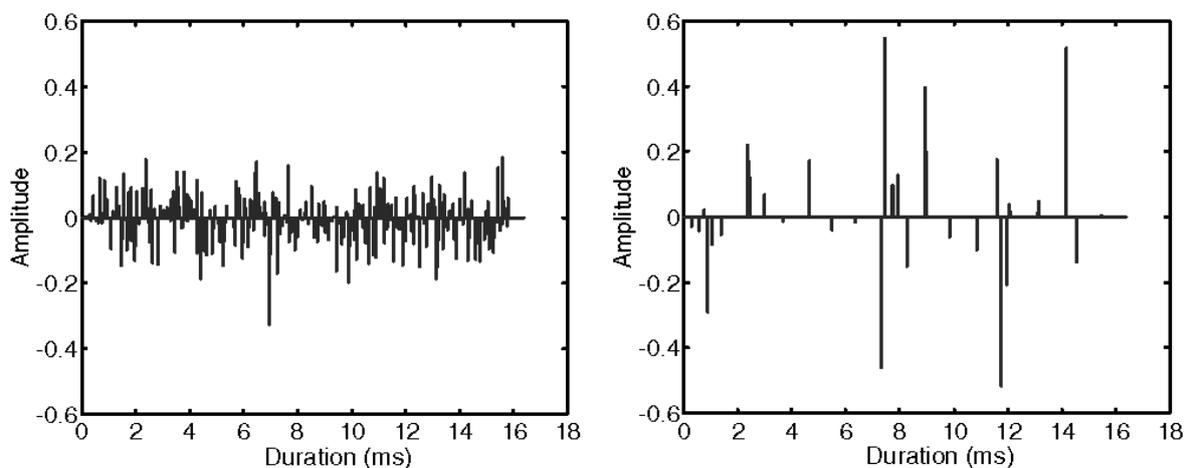
Figure 0.2: Illustration of two artificial impulse responses with different roughness. Left: a smooth IR like it might be featured by a conifer. Right: a rough IR like it might be featured by a broad-leafed tree.

large reflective surfaces will produce a rough IR, whereas the small leaves of a conifer will produce many reflections with low amplitude, which will result in a smooth IR.

If bats would be able to use this IR roughness, this would indeed allow them to discriminate and classify trees and other large and complex objects, and enable them to use said objects as navigational landmarks (see figure 0.3). However, the IR roughness is a completely statistical parameter, and therefore not so easily to utilize as, for example, the spectral interference pattern mentioned above.

Still, we were indeed able to show a few years ago that the bat *Phyllostomus discolor* is in fact able to classify IRs according to their roughness (Grunwald et al., 2004). However, open questions remained: how sensitive is the bats' roughness discrimination, and is there a lower limit to it? Just how "rough" must an echo be, so that successful evaluation is possible? This topic is investigated in chapter 1.

Also in 2004, Wolfram-Peter Stilz published his thesis, in which he examined the echo-acoustical parameters of natural objects in a free-field study. His data revealed which shape the actual IRs of natural objects indeed have. In chapter 2, we measured the roughness-discrimination ability of *P. discolor* again, only this time with IRs that were - based on Stilz' data - more naturally designed . The obtained results should allow a comparison with the actual roughnesses of natural vegetation as measured by Stilz, and therefore show if the magnitude of the bats' roughness discrimination ability is indeed sufficient for natural conditions.
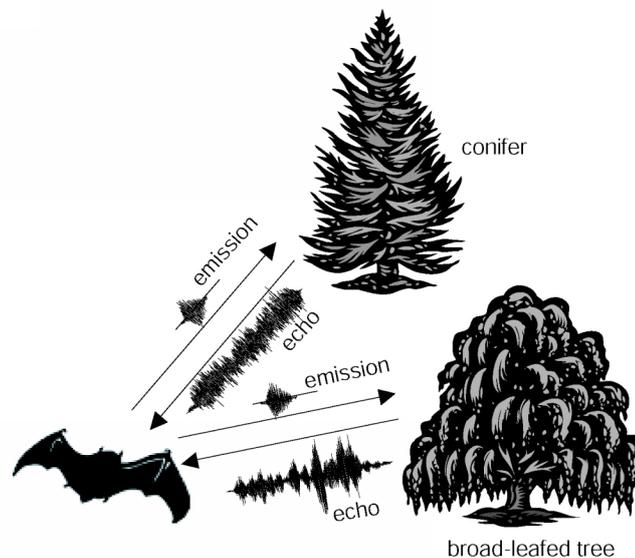
Figure 0.3: Illustration of the sonar emissions and the different echoes a bat may receive from different foliage types. Note the rather smooth envelope structure of the conifer's echo and the comparatively rough envelope structure of the broad leafed tree's echo.

In chapter 3, we investigate a different aspect of an echo's time domain. As already mentioned above, there is by now some evidence for a bat's ability to extract the ensonified object's IR from the echo (Weissenbacher & Wiegrebe, 2003). However, the discussion about the actual procedure is still open, mainly focusing on the question if the extraction is done in the time domain (for example via a cross-correlation, as stated above) or in the frequency domain by a multiplication of the magnitude-spectra and an addition of the phase-spectra. It is a fact that every auditory signal, after passing the bat's auditory periphery, is converted into a combination of time and frequency domain, the auditory spectrogram. This auditory spectrogram represents therefore the basis for the actual extraction process, which hence has to evaluate both time and frequency domain aspects. Especially a bat's sensitivity for the temporal aspects of an echo, that is the echo's phase, has already been examined in several studies and has been the topic of a controversial discussion since (Beedholm, 2006; Beedholm & Mohl, 1998; Menne et al., 1989; Moss & Schnitzler, 1989; Moss & Simmons, 1993; Pollak, 1993; Simmons, 1979, 1993; Simmons et al., 1990a, 2003). We undertook a different, new approach in the investigation of phase sensitivity, which will hopefully provide some new facts for this discussion.

The application of virtual objects in playback experiments

Due to the very specific echo-acoustical parameters that are of interest in our experiments, it was not possible, respectively advisable, to use real targets, as it was done in a multitude of experiments concerning echolocation (for examples see (Habersetzer & Vogler, 1983; Simmons, 1971; Simmons et al., 1974; Simmons & Vernon, 1971; von Helversen, 2004)). The employment of real targets has the disadvantage of hardly allowing a complete control over all its acoustical parameters, like e.g. amplitude or spectral composition. This is especially impedimental regarding the objective of our experiments. Both roughness- as well as the phase-sensitivity experiments concentrate on one crucial parameter of an echo, and therefore require a preferably high dependability that only this parameter can be used by the bat during the experiment. This cannot be ascertained when using real targets, especially as the targets used in chapter 1 and 2 are supposed to represent rather large trees and bushes that would have to be exchanged between trials.

Modern digital signal processing technology today offers a solution for this by allowing near real-time finite impulse response (FIR) filtering even at high sample rates, thereby providing the tools for creating artificial echoes of real or virtual targets in the ultrasonic range. In doing so, recorded echolocation calls from the animals are computed with an IR from an object stored in a computer, resulting in the echo of an object that is not really present or even existent: a virtual object. A cross-correlation of an artificial echo generated this way with the corresponding real one shows a cross-correlation-coefficient of 0.95 to 0.99 (Aubauer & Au, 1998), which demonstrates the highly significant similarity between the two echoes. Several experiments with dolphins proved that the animals treated artificial echoes identical to real echoes (Aubauer & Au, 1998; Aubauer et al., 2000). Recent studies demonstrated that the virtual-target-method is also applicable for bats (Firzlaff et al., 2006, 2007; Grunwald et al., 2004; Weissenbacher & Wiegrebe, 2003). As the utilized IR can be easily created using a simple computer program, the experimenter obtains full control over all of the IR's acoustical properties and is thus able to conduct very precise modifications of the relevant parameter alone.

For all of the following experiments we therefore used a basic setup as depicted in figure 0.4. The character of the rewarded respectively unrewarded IR differs for every experiment (illustrated in more detail in the method section of each chapter); the combination of microphones, digital acquisition processors (DAP) and speakers allows the generation of the virtual targets and hence take the place of the real targets.
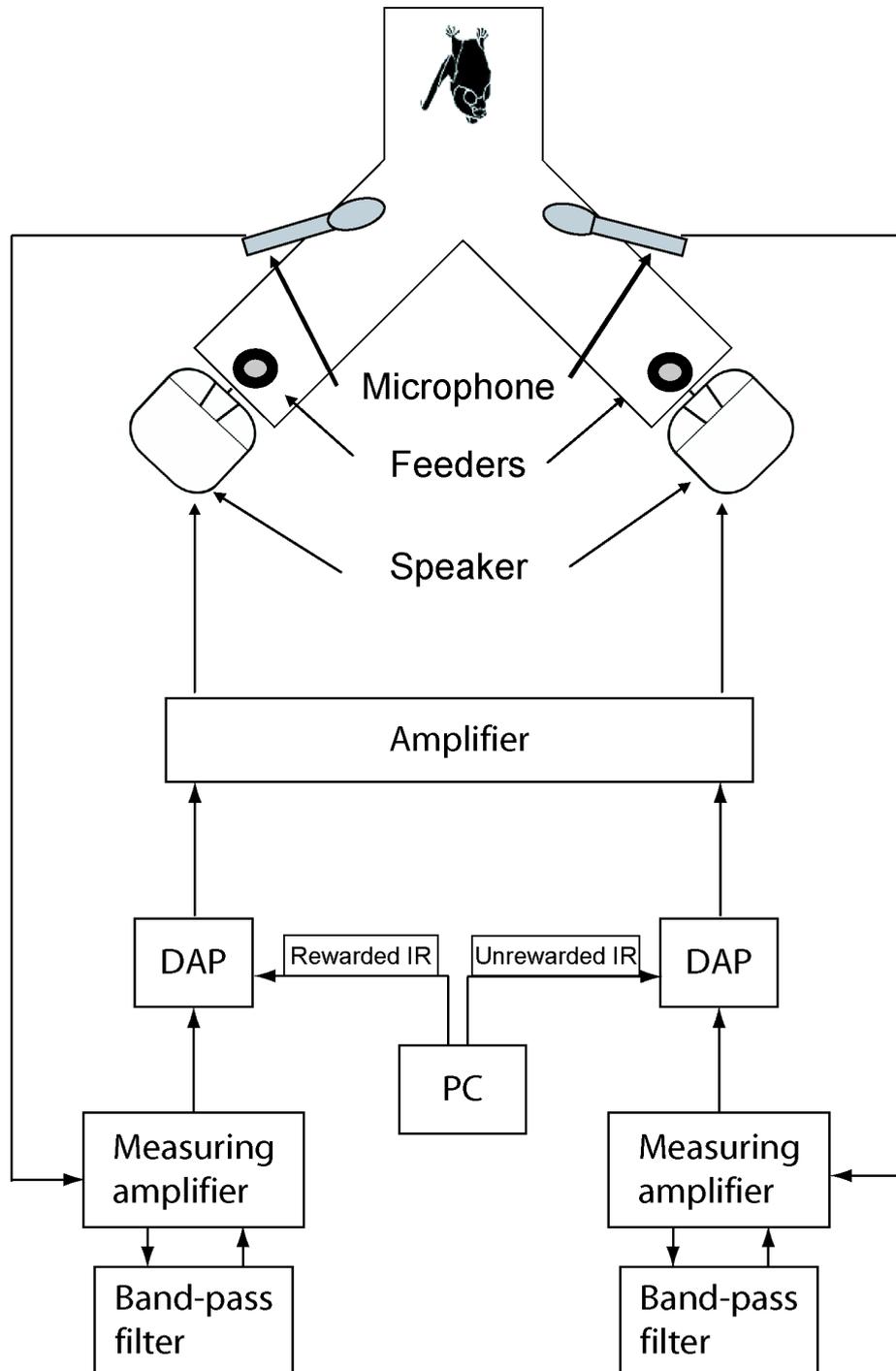
Figure 0.4: Schematic of the experimental setup. The bat's echolocation call is recorded by both microphones, amplified, filtered, and fed into each of the two data-acquisition-boards. There, the echolocation call is convolved with a smooth IR on one channel and a rougher IR on the other, then amplified again and played back to the bat via ultrasonic speakers. The bat then has to crawl towards the speaker where the echo containing the smooth IR originated in order to obtain a food reward.

1 A neural correlate of stochastic echo imaging

This chapter was published in 2006 by Uwe Firzlaff*, Sven Schörnich*, Susanne Hoffmann, Gerd Schuller, and Lutz Wiegrebe; in the Journal of Neuroscience (Vol. 26(3),pp 785-791, *=contributed equally)

Uwe Firzlaff designed the neurophysiological experiment and conducted it together with Susanne Hoffmann. Neurophysiological data analysis was conducted by Uwe Firzlaff, Susanne Hoffmann and Lutz Wiegrebe. Gerd Schuller provided the equipment for the neurophysiologial setup. The psychophysical experiment was designed by Lutz Wiegrebe and myself. I did the implementation and psychophysical data analysis. The parts of the manuscript concerning the psychophysical experiment were written by myself, the parts concerning the neurophysiological experiment were written by Uwe Firzlaff. Introduction and discussion were written by Uwe Firzlaff, Lutz Wiegrebe and myself in close collaboration.

1.1 Abstract

Echolocating bats quickly navigate through a highly structured environment relying on echolocation. Large natural objects in this environment, like bushes or trees, produce complex stochastic echoes, which can be characterized by the echo roughness. Previous work has shown that bats can evaluate echo roughness to classify the stochastic properties of natural objects. This study provides both psychophysical and electrophysiological data to identify a neural correlate of statistical echo analysis in the bat *Phyllostomus discolor*. Psychophysical results show that the bats require a fixed minimum roughness of 2.5 (in units of base-ten logarithm of the stimulus 4th Moment) for roughness discrimination. Electrophysiological results reveal a subpopulation of 15 out of 94 recorded cortical units, located in an anterior region of auditory cortex, whose rate responses changed significantly with echo roughness. It is shown that the behavioral ability to discriminate differences in the statistics of complex echoes can be quan-

titatively predicted by the neural responses of this subpopulation of auditory-cortical neurons.

1.2 Introduction

Through echolocation, a bat can not only find out about the position of an object in the dark, but also about its structure, which is encoded as the objects acoustic image within the echo. The acoustic image of an object is the sum of the reflections in response to an acoustic impulse of theoretically infinite shortness and infinite amplitude (Dirac impulse); it is called the object's impulse response (IR). Technically, the echo a bat will perceive is the convolution of the bat's sonar emission and the IR.

Larger natural objects like trees have a very complex structure with thousands of reflective surfaces which are provided by the leaves and branches. Moreover, this structure (and thus its IR) will be highly unstable over time because movements of the leaves due to wind will occur and a bat will rarely encounter a tree twice from exactly the same angle. Echoes reflected from these surfaces will have no systematic spectral interference pattern.

However, a bat should be able to identify natural objects in order to navigate within complex surroundings or, in the case of frugivorous bats, for the classification of trees which provide food. A comparative analysis of the IRs of two different trees has indicated that the degree of envelope fluctuation of the IRs, i.e., the IR roughness, is a good predictor for the correct association of the IRs to the corresponding tree (Müller & Kuc, 2000). A broad-leafed tree with few but large reflective surfaces will produce a rough IR, whereas the small leaves of a conifer will produce many reflections with low amplitude, which will result in a smooth IR. A free-field study confirmed the high predictive power of the IR roughness for the classification of natural objects (Stilz, 2004).

In a psychophysical playback experiment with phantom objects, Grunwald et al. (2004) have shown that the fruit-eating bat *Phyllostomus discolor* can learn to discriminate echoes generated with a smooth IR from echoes generated with a rough IR and that once they had learned this discrimination, *P. discolor* spontaneously classified unknown IRs according to IR roughness. Simulations of these results suggested that modulation-sensitive neurons in the midbrain with best modulation frequencies above about 80 Hz could provide a neural basis for this performance. Neural processing of echo roughness has not been studied so far. It is especially interesting to directly relate neural process-

ing to behavioral performance, an attempt which has only been made a few times in bats (Riquimaroux et al., 1991, 1992).

Thus, two questions are pursued here: (a) what are the thresholds for auditory-object discrimination based on IR roughness in *P. discolor* and (b) is there an auditory cortical correlate of the behavioral performance? The first question is addressed with a psychophysical phantom-object experiment. The second question is addressed with electrophysiological recordings from neurons in the auditory cortex of *P. discolor* with a stimulation paradigm that closely matches the psychophysical paradigm.

1.3 Methods:

1.3.1 Animals:

The experimental animal, the lesser spear-nosed bat *P. discolor*, forages for fruit, nectar, pollen, and insects in a neotropical forest habitat and navigates through highly structured surroundings. *P. discolor* emits brief (<3 ms), broad-band multiharmonic echolocation calls covering the frequency range between 40 and 90 kHz.

1.3.2 Psychophysics:

The psychophysical experiments were implemented as virtual-object playback experiments. The bats were required to evaluate the echoes of their echolocation calls. These echoes were generated by convolving in real time the calls with the acoustic impulse response of a virtual object. Thus, unlike in classical psychoacoustic experiments, the bats did not hear sounds unless they emitted echolocation calls.

Four female bats were used for the psychophysics. All four animals were housed together with access to water ad libitum, except during individual training sessions. Training sessions were usually conducted 5 days per week, followed by a 2 day break. On training days, the bats received food only as a reward (consisting of banana pulp) in the training setup. On the days without training they had access to mealworms (larvae of *Tenebrio molitor*) ad libitum.

1.3.2.1 Impulse responses:

We created complex IRs with different degrees of roughness, similar to a previous experiment (Grunwald et al., 2004). Each IR consisted of sparse noise, which is generated by

inserting random-width temporal gaps between the amplitude values of Gaussian noise (Hübner & Wiegrebe, 2003). All IRs generated this way had chaotic waveforms (see figure 1.1, first column) and frequency-independent (white) magnitude spectra (data not shown). Thus, the magnitude spectra do not vary systematically with IR roughness. When such an IR is convolved with an echolocation call, the resulting echo has the magnitude spectrum of the echolocation call (see figure 1.1, third column) because a convolution in the time domain corresponds to a multiplication in the frequency domain.

IR roughness was quantified in terms of the fourth moment (M4; the IR wave form raised to the power of four divided by the squared wave form raised to the power of two) (Hartmann & Pumplin, 1988). Roughness values are given as the base 10 logarithm of the M4 (log10M4). The IRs were sorted into 31 groups ranging from a roughness of 0.5 to 3.5 (log10M4). Each group contained 25 different IRs of the same roughness, giving a total of 775 IRs, thereby ensuring that each IR was rarely presented twice. All IRs had the same root-mean-square amplitude. At a sampling rate of 250 kHz, the IRs had a duration of 14.4 ms, equivalent to an object depth of 2.5 m.
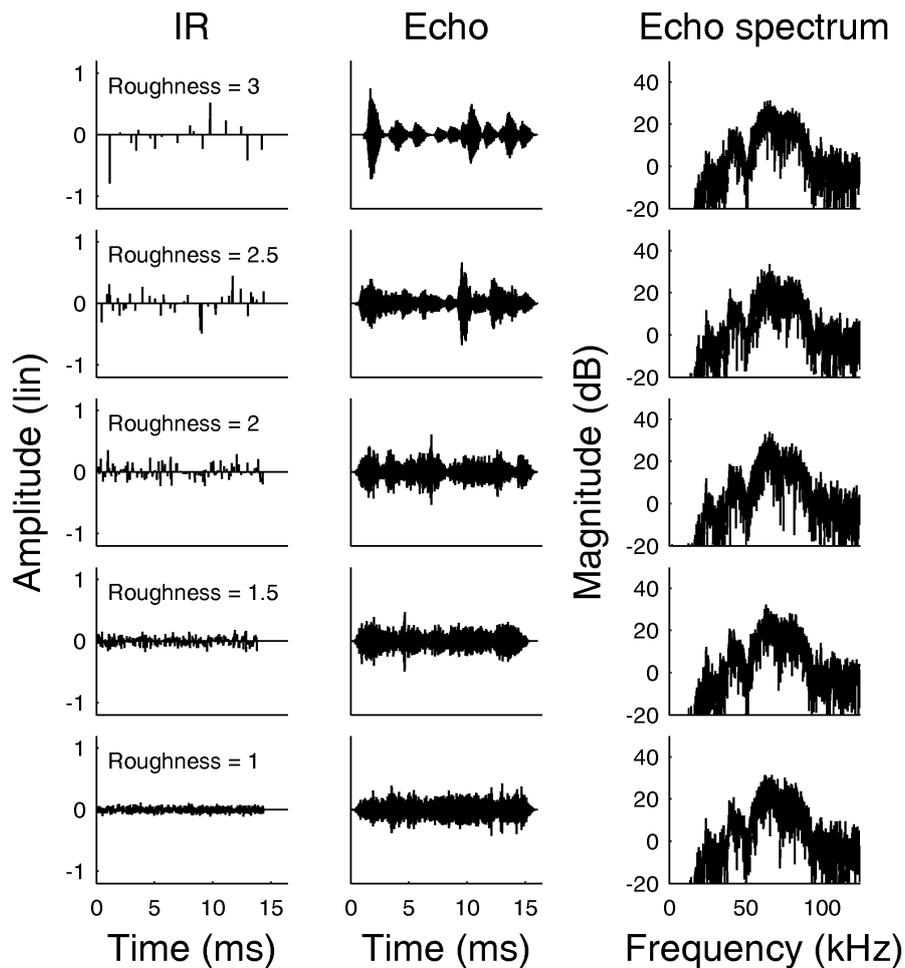
Figure 1.1: Examples from the stimulus set for the psychophysical experiments in *P. discolor*. The first column shows the IRs used to generate the echoes in the psychophysical playback experiment. The roughness of the IRs, quantified as the base 10 logarithm of the waveform's 4th Moment is shown in each panel. The second column shows echoes generated from the IRs in the first column with a standard *P. discolor* echolocation call. The magnitude spectra of the echoes are shown in the third column. Note that the magnitude spectra and the overall sound-pressure level are independent of roughness.

1.3.2.2 Experimental Setup:

The bats were trained in a two-alternative, forced-choice playback setup (see figure 0.4). It consisted of a Y-shaped maze, inversely mounted on the wall of an echo-attenuated chamber at an angle of 45 degrees. The starting perch was located at the upper end. In each branch, a reward feeder, a 1/4"' microphone (B&K Instruments 4135, Naerum, Denmark), and a speaker (Matsushita EAS10 TH800D, Osaka, Japan) were mounted facing towards the starting perch. During the experiment, the emitted echolocation calls were recorded by both microphones. Each microphone output was amplified (B&K 2610), band-pass filtered (30-100 kHz, Krohn Hite 3550, Brockton, MA, USA), and digitized by a data-acquisition board (Microstar DAP 5200a, Bellevue, WA, USA) at a sampling rate of 250 kHz. The boards convolved the input with two different IRs (a smooth reference IR on one side and a rougher test IR on the other) on the DAP-boards by zero-padding both the recorded call and the IRs to 4096 samples and multiplying the complex spectra of recorded call and IR. This procedure corresponds to the formation of an echo of a phantom object, that is to say, every change in the bat's echolocation call results in an immediate change in the artificial echo. The artificial echo was amplified (Harman/Kardon 6110, Château du Loir, France) and played back to the bat after a total delay of 18 ms, corresponding to a target distance of about 3 m.

1.3.2.3 Procedure:

All four bats were trained to discriminate IR roughness in a two-alternative, forced-choice paradigm. To obtain a food reward, the bats had to crawl towards the end of that branch of the Y maze where the echo generated with the reference roughness-IR originated. The test IR roughness was always higher than the reference roughness. When the bats' performance exceeded 80% correct in this discrimination task, psychometric functions were obtained. Whereas the reference roughness was kept constant, the test roughness was changed randomly. The stochastic IRs were refreshed for every presentation. Each point of the psychometric function is based on 30 trials. Discrimination threshold was set to 75% correct which, on the basis of 30 trials, corresponds to a significance level of $P < 0.003$. The experiment was repeated four times with four different reference roughnesses, namely 0.5, 1.8, 2.5 and 2.8 (log10M4).

1.3.3 Neurophysiology

1.3.3.1 Surgery

All experiments complied with the principles of laboratory animal care and were conducted under the regulations of the current version of the German Law on Animal Protection (approval 209.1/211-2531-68/03, Reg. Oberbayern). The principle surgical procedure has been described in detail elsewhere (Schuller et al., 1991). In brief, bats were anesthetized using a combination of Medetomidin, Midazolam and Fentanyl (MMF, 0.4 μg, 4 μg and 0.04 μg per gram body weight, respectively). The skin overlying the skull was opened along the midline and the skull surface was freed from tissue. A small metal tube was fixed to the skull using a microglass composite in order to fixate the animal to a stereotaxic device, and the accurate skull position in stereotaxic coordinates was determined as described in details elsewhere (Schuller et al., 1986).

1.3.3.2 Stimulus production and recording of neural responses:

Experiments were conducted in an anechoic chamber. Acoustic stimuli were computer generated (Matlab, Mathworks, Natick, MA), digital-analog converted (RV8, Tucker Davis Technologies (TDT), Gainesville, Fl, sampling rate: 400 kHz), filtered and attenuated (TDT FT-6, PA5) and binaurally presented via custom-made ultrasonic earphones with a flat frequency response (+3 dB) between 10 and 100 kHz (Schuller, 1997). Stimuli consisted of a typical echolocation call of *P. discolor* (frequency range: 40 to 90 kHz) convolved with a stochastic IR. After the convolution, the stimuli had a duration of 18 ms. 50 IRs in five groups of roughness were used (log10M4 = 1.8, 2.0, 2.3, 2.5, 2.8), i.e., in the range of the behavioral experiments. Stimuli were randomly presented at 20 to 30 dB above a neuron's pure-tone threshold with 10 to 20 repetitions of the entire set and a silent interval of 10 ms before stimulus onset. Repetition rate was 1.3 Hz.
Action potentials from neurons in the auditory cortex of three lightly anaesthetized bats were recorded extracellularly using glass microelectrodes filled with 2 M NaCl and 4% Pontamine Sky Blue (3-8 M impedance). As it was not always possible to clearly discriminate the activity of a single neuron, the term unit will be used in the following to describe the collective activity of one to three neurons recorded at a recording site. Neural activity was monitored audiovisually, and threshold and best frequency of a unit were roughly determined. Action potentials were amplified using conventional methods and recorded using an AD converter (RP2.1, TDT, sampling rate: 25 kHz) and

Brainware (TDT). Electrode penetrations were tangential to the brain surface. After the completion of an experiment, lesions were made to the brain in order to reconstruct the position of recording sites from subsequent histological processing in standardized coordinates of a brain atlas of *P. discolor* (Nixdorf, Fenzl, Schwellnus, unpublished).

1.3.3.3 Data analysis

Spike responses from all 50 stimuli were displayed as peri-stimulus time histograms (PSTH, 1 ms bin-width) and raster plots. Units typically responded with an onset response followed by a clearly distinguishable sustained response component. As will be seen below, the onset response occurred with each of the 50 stimuli independent of roughness. Therefore, it was excluded from further analysis by setting a time window containing only the sustained response. Size and position of the window were derived from the PSTH. The analysis window started immediately after the end of the onset response and ended when the sustained response level reached the level of spontaneous activity. Spontaneous activity was derived from the 10-ms time window preceding stimulus onset. Responses to stimuli from each of the five roughness groups were tested for statistical significant differences using a Kruskal-Wallis Test with a correction for multiple testing (Matlab Statistics Toolbox). Significance was set at $P < 0.05$.

1.4 Results

1.4.1 Psychophysics

A psychometric function for IR roughness discrimination with a reference roughness of 1.8 (in units of log10M4) is shown in the inset of figure 1.2. Data are averaged across the four animals. The function shows that for a reference roughness of 1.8, the bats need a test roughness of at least 2.5 to reliable discriminate IR roughness.

The four horizontal bars present the summary results for the four values of reference roughness. Each bar shows the minimal roughness-difference needed to significantly discriminate IRs with the test roughness from IRs with the reference roughness. These results show that there is a fixed behavioral threshold for IR roughness discrimination: A roughness of about 2.5 is required by the bats to reliably discriminate an IR with this roughness from a smoother one. Above this threshold, discrimination performance improves substantially.
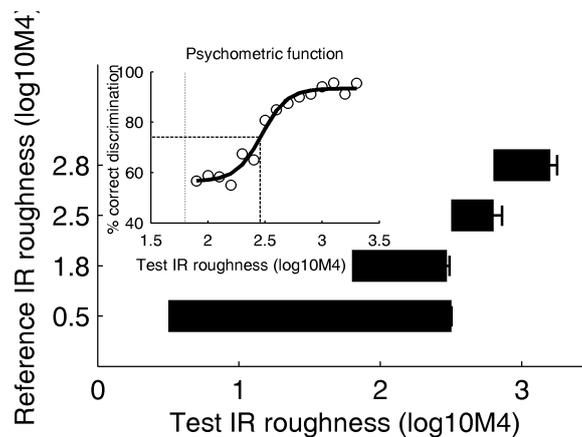
Figure 1.2: Results of the psychophysical experiments. The inset shows a psychometric function for IR-roughness discrimination (open circles). The reference IR roughness was 1.8 (vertical dotted line). The discrimination threshold was determined by fitting a sigmoid function (strong solid line) and extracting the 75% correct value (dashed lines). The horizontal bars show the average results for the four values of reference roughness. The left end of each bar shows the reference roughness, and the right end shows the discrimination threshold. Error bars represent across-animal standard errors.

1.4.2 Neurophysiology

Results are based on 94 cortical units. All units responded well to frequencies in the range of the echolocation calls of *P. discolor* (40-90 kHz). 15 out of 94 units responded significantly different to stimuli with different degrees of roughness (p < 0.05, Kruskal-Wallis nonparametric one-way analysis of variance). The raster plot and the summary PSTH in figure 1.3 reveal a strong onset response followed by a variable degree of sustained activity. For the response-strength analysis, only the sustained activity was used. The analysis window was terminated when the level of spontaneous activity was reached. The range of analysis-window durations of all roughness-sensitive units was from 19 to 126 ms (median 34 ms). The stimulus duration was 18 ms. Thus, the analysis window was often considerably longer than the stimulus duration.

Examples of responses of four units whose firing increases significantly with increasing stimulus roughness are shown in the right panels of figure 1.3. Note that the stimuli with different roughness share the same sound-pressure level and the same power spectrum (cf. figure 1.1). Except for one unit, all units with significant roughness coding responded stronger to stimuli with higher roughness. This is shown in a summary plot of all units in Fig 1.4. The regression line for roughness-sensitive units has a signifi-
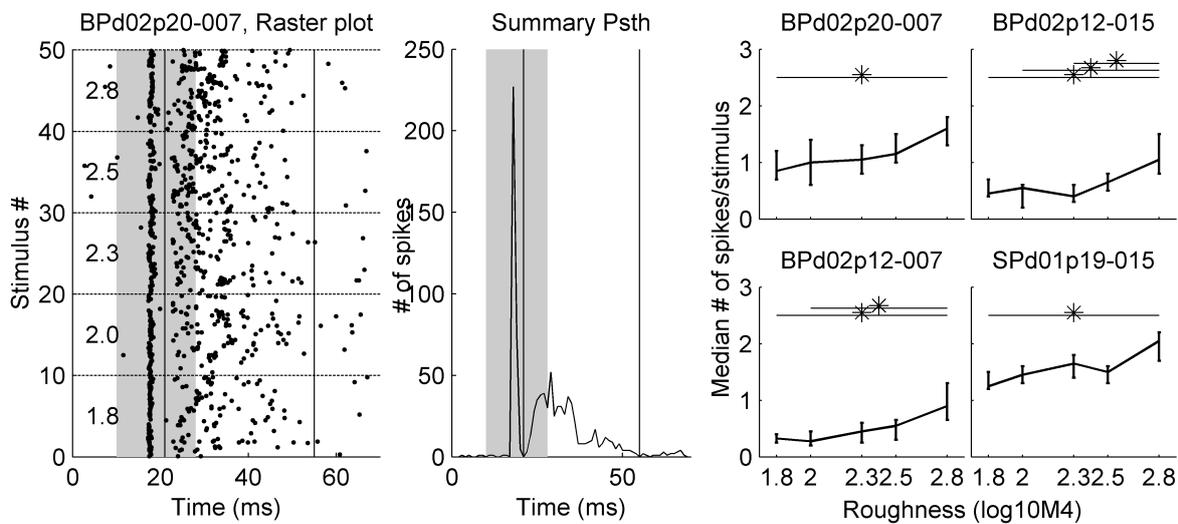
Figure 1.3: Electrophysiological results. The left plot shows a raster plot of a roughness-sensitive unit to 10 repetitions of all 50 stimuli; the middle plot shows the PSTH summed over all stimuli and repetitions. The summary PSTH was used to exclude the onset responses from additional analysis by setting a time window (vertical solid lines in the PSTH and raster plot), which started immediately after the end of the onset response and ended when the sustained response level reached the level of spontaneous activity. The time of stimulus presentation is indicated by the gray area in the PSTH and raster plot. Response strength as a function of IR roughness is shown for four roughness-sensitive units in the auditory cortex of *P. discolor* in the four panels on the right. Response strength is shown as the median number of spikes per stimulus across 10 different echoes sharing the IR roughness given on the abscissa. Vertical bars represent the range of the 25 and 75% percentile. Significant response differences (Kruskal-Wallis test, p<0.05) are indicated by the horizontal lines and asterisks.
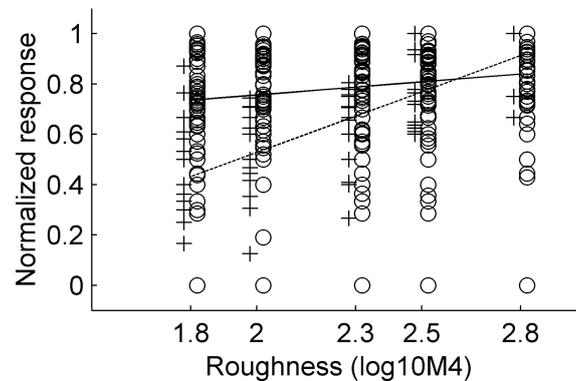
Figure 1.4: Comparison of the regression lines of response strength calculated for all 14 roughness-sensitive units for which responses increased with increasing roughness (dashed line) and all nonsensitive units (solid line). IR roughness is shown on the abscissa, and normalized response strength is shown on the ordinate. The crosses show normalized response strength for roughness-sensitive units, and the circles show response strength for nonsensitive units. The slope of the regression line is significantly steeper for the roughness-sensitive units, indicating that the response of sensitive units increases with IR roughness ($p<0.001$; ANCOVA). The slope of the regression line of the roughness-insensitive units is very shallow, showing that, for these units, the response strength is not correlated with IR roughness.

cantly steeper slope compared to the regression line for non-sensitive units (ANCOVA linear regression, Matlab signal processing toolbox, $p < 0.001$).

The relative Strengths of onset and sustained responses do not correlate to the ability of the units to encode echo roughness. In 70 out of the 94 units, the onset-response magnitude was weaker than the sustained response; in 24 units the opposite was true. Of the 14 roughness-sensitive units in which responses increased significantly with increasing roughness, eight had a stronger onset response than sustained response, the other six had a stronger sustained response. The recordings were derived from locations covering a distance of about 3500 μm along the rostro-caudal axis and about 3000 μm along the dorso-ventral axis (cf. figure 1.5), which corresponds to the neuroanatomically evaluated dimension of the auditory cortex of *P. discolor* (S. Radtke-Schuller, personal communication). Units with significant responses to roughness were not uniformly distributed on the auditory cortical surface but were almost exclusively located in anterior regions of auditory cortex (figure 1.5). The only unit that responded stronger to smooth stimuli was located in the posterior part of the auditory cortex.

The clustering of sensitive units in anterior parts of the auditory cortex also means that the relative percentage of sensitive unit is underestimated when calculated for the total
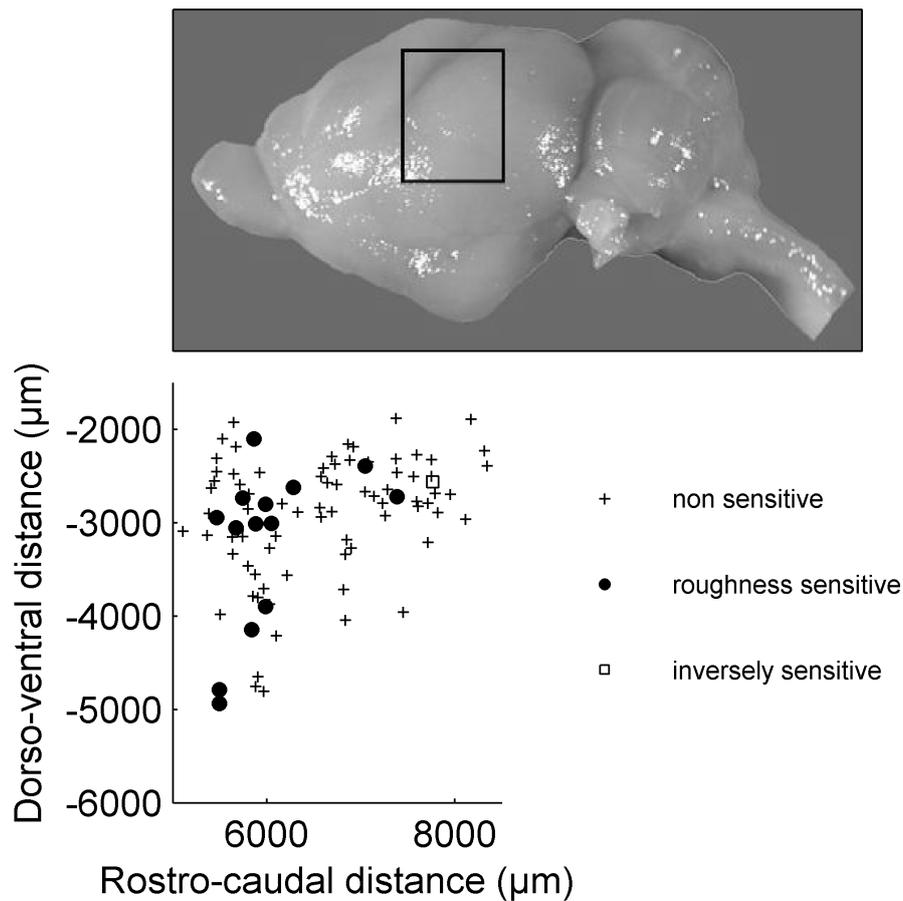
Figure 1.5: Location of recording sites in the auditory cortex of *P. discolor*. The limits of the scatter plot are superimposed on a photograph of the *P. discolor brain*. Units that were not significantly sensitive to IR roughness are shown as crosses, and roughness-sensitive units are shown as filled circles. The one open square represents a single unit that showed inverse roughness sensitivity (i.e., the rate response decreased with increasing IR roughness).

cortical area scanned in our experiments. The relative density of roughness-sensitive units would increase if only calculated for the anterior parts, however, as we do not yet have the accurate anatomical limits of different cortical fields such an analysis was not yet possible.

1.4.3 Comparison of psychophysics and neurophysiology

In order to compare the psychophysical discrimination performance and the roughness sensitivity of cortical units, a Receiver Operating Characteristics (ROC) analysis was used (Britten et al., 1992; Green & Swets, 1966) to generate a neurometric function along the same axes as the psychometric function. The neurometric function reflects the probability that an ideal observer could accurately discriminate IR roughness basing his judgments on responses like those recorded from the units under study.

The ROC analysis was performed by generating a so-called ROC curve for the comparison of each signal condition (roughness > 1.8 log10M4) and the standard condition (roughness = 1.8 log10M4). The ROC curve shows the probability that both the rate response in a signal condition and the response in the standard condition exceed a certain threshold, e.g., one spike per stimulus. This probability was plotted as a function of the height of the threshold. From there, the (neural) percent correct discrimination for each signal condition was generated by calculating the area under the ROC curve. For the current comparison, we pooled the responses of all 14 units whose response increased significantly with IR roughness. The resulting neurometric function is shown together with a re-plot of the psychometric function with a reference roughness of 1.8 log10M4 in figure 1.6. The analysis shows that there is a good agreement between the psychophysical performance and the ideal-observer performance based on the subgroup of roughness sensitive units. Note that the psychometric function for a reference roughness of 0.5 log10M4 was very similar to that for a reference of 1.8 log10M4 indicating that the animals could not discriminate roughness below 1.8 log10M4. The neurophysiological data set was therefore limited to the roughness region between 1.8 and 2.8 log10M4.
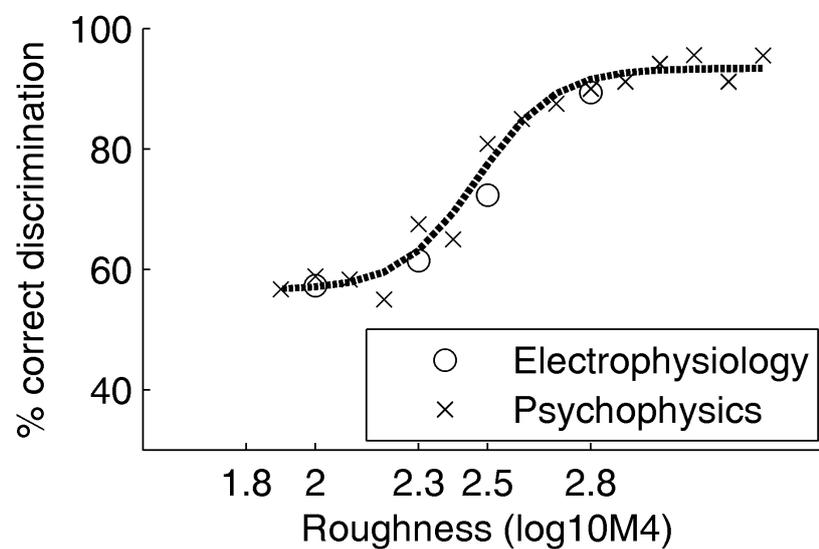
Figure 1.6: Comparison of the psychophysical and neurophysiological roughness discrimination performance. The crosses show the psychophysical performance with a reference roughness of 1.8 log10M4; the dotted line is a sigmoidal fit to the psychophysical data. The open circles show the performance of an ideal observer (using a receiver-operating-characteristics analysis) basing its decisions on the pooled responses of the 14 roughness-sensitive cortical units found in this study.

1.5 Discussion

In the present study, neurons were found in anterior regions of the auditory cortex of the bat *P. discolor* that encoded echo roughness in their response strength. The performance of these neurons closely matched the bats' behavioral sensitivity to echo roughness as a physiological correlate to statistical echo analysis in the auditory cortex.

Because the exact partitioning of the auditory cortex and the location of different cortical fields is not yet known for *P. discolor*, the location of roughness-sensitive units in the auditory cortex cannot be precisely attributed to defined cortical areas. However, Esser & Eiermann (1999) have investigated the organization of the auditory cortex in a closely related phyllostomid bat species *Carollia perspicillata*. They described six different auditory fields including the primary auditory cortex (AI), a rostrally adjoining anterior auditory field (AAF), and two dorsally located auditory fields. It can be assumed that the general organization of the auditory cortex is not very different in *P. discolor*. Roughness-sensitive units were found mainly in anterior regions over the whole dorsoventral distance. Thus, roughness-sensitive units seem to be mainly located in two cortical fields, probably representing the AAF and an anterior dorsal field. Only a few recordings were derived from units in posterior ventral regions where the AI might be located, so no clear assertion about encoding of echo roughness can be made for neurons in the AI.

Complex response patterns consisting of a phasic onset response followed by a sustained excitatory response have been described for neurons in the inferior colliculus (IC) and the auditory cortex of various mammals (Brosch & Scheich, 2003; Geisler et al., 1969; Heil, 1998). Several studies showed that different stimulus features can be differentially encoded by onset and sustained-response components. Heil (1998) showed that binaural envelope transients are encoded by the onset response of neurons in the inferior colliculus of rats, whereas the binaural combination of steady state intensities is encoded by the sustained response. For the auditory cortex, it was also shown that the onset-response strength is related to the rising-envelope slope rather than to the steady-state intensities (Heil, 1997; Heil & Irvine, 1998). Ahissar et al. (1992) showed that the majority of motion-sensitive neurons in the auditory cortex of awake monkeys showed motion sensitivity in their sustained components. These findings support our results: whereas the stimulus onset evoked a strong onset response independent of roughness, the sustained response was highly dependent on stimulus roughness.
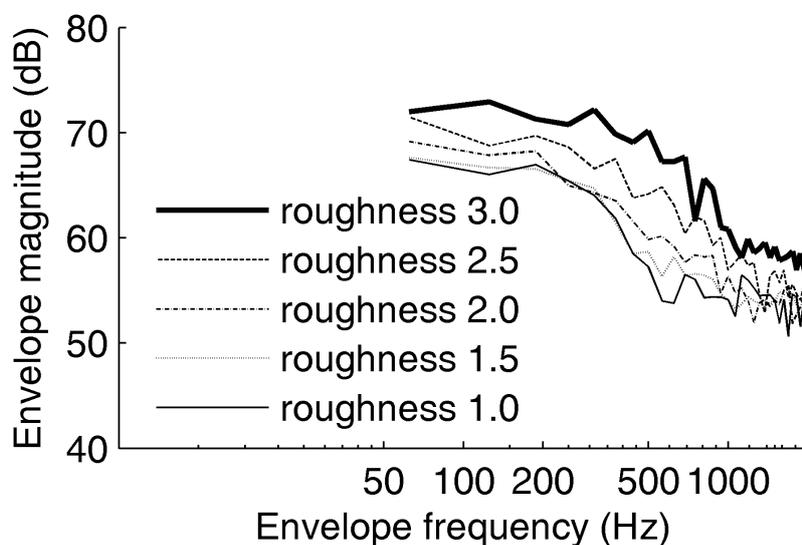
Figure 1.7: Envelope magnitude spectra of echo stimuli presented in the neurophysiological experiments. Unlike the magnitude spectra of the waveform (compare figure 1, right column), the envelope spectra vary systematically with roughness. With increasing roughness, the envelope magnitude increases for all envelope frequencies; however, the increase is most pronounced in the envelope-frequency range, ≈ 500 Hz.

Grunwald et al. (2004) argued that modulation-sensitive units possibly located in the inferior colliculus may play a role in the processing of echo roughness. Physiological modulation sensitivity has mainly been tested with sinusoidally amplitude-modulated (SAM) stimuli. The envelope spectra of these stimuli (the magnitude spectra of their Hilbert envelopes) are narrow band and they show a pronounced peak at the modulation frequency. The envelope spectra of the stimuli used in this study differ substantially. Because of the aperiodic and transient nature of the IRs, the envelope spectra of the echoes are broad band and with increasing roughness, the envelope magnitude increases for all modulation frequencies. The systematic effect of echo roughness on the envelope spectra is shown in Figure 1.7. The roughness dependent changes are most prominent in the envelope-frequency region ≈ 500 Hz.

The IR roughness sensitivity investigated in this study is, thus, most closely related to modulation-depth sensitivity rather than to modulation-frequency sensitivity, per se.

Human psychophysical sensitivity to the modulation depth of SAM noise has been measured first by Wakefield & Viemeister (1990). Later studies ((Ewert & Dau, 2004) confirmed for a broad stimulus set that, above the SAM detection threshold, modulation-

depth discrimination is constant at 1 dB. Although there are no data on modulation-depth discrimination in bats, the envelope spectra of the current stimuli (figure 1.7) indicate changes in the envelope spectra clearly exceeding the human 1 dB threshold.

Krishna & Semple (2000) investigated responses of inferior colliculus neurons in the Mongolian gerbil to SAM tones varying in both modulation frequency and modulation depth. They showed that the rate modulation transfer function depended significantly on modulation depth. Dependent on modulation frequency, changes in modulation depth could result in either suppression or enhancement of the rate responses. Thus, Krishna & Semple (2000) demonstrated that at the level of the inferior colliculus, some units can encode modulation depth. However, as outlined above, the envelope spectra differ substantially from those of our stimuli.

Stimuli that are more similar to ours have been used by Kvale & Schreiner (2004) in the inferior colliculus of cats. They used pure-tone carriers modulated with an 800 Hz rectangular modulator and stochastic modulation-depth variations. Like our current stimuli, these stimuli have a broad-band envelope spectrum. Also similar to a roughness increase in our current stimuli, an increase in the variance of modulation depth results in an increase of the envelope magnitude for this broad range of envelope frequencies. Kvale and Schreiner showed that neurons in the inferior colliculus can detect dynamic changes in variance of their modulation depth distribution in their firing rate. These studies suggest that roughness-related response changes may exist at the level of the inferior colliculus in the bat *P. discolor*.

To our knowledge, modulation-depth coding has not been studied at the level of the auditory cortex. Figure 1.7 shows that sensitivity to relatively high-modulation frequencies ≈ 500 Hz is a prerequisite for the encoding of IR roughness. Therefore, tuning to modulation frequency cannot be ignored in this context. Schreiner & Urbas (1988) found that neurons in the AAF of cats had highest best modulation frequencies for both phase-locked and rate responses, whereas best modulation frequencies in AI and the posterior auditory field were markedly lower. Thus, the localization of roughness-sensitive units in anterior parts of the auditory cortex of *P. discolor* resembles the representation of high-frequency amplitude modulations in the auditory cortex of the cat.

Phase locking in auditory-cortex neurons to SAM is limited to low-modulation frequencies (Langner, 1992). Previous reports suggest that various cellular and network properties such as adaptation and synaptic depression may underlie this low-pass response behavior (Joris et al., 2004; Wehr & Zador, 2005). However, Lu et al. (2001) showed that

a distinct population of neurons exists in the auditory cortex of marmosets that encodes high-modulation frequencies as a rate code. A rate code for high-modulation frequencies in the auditory cortex was also reported in other studies (Bieser & Muller-Preuss, 1996; Liang et al., 2002; Lu & Wang, 2004). Our current results suggest that neurons in the auditory cortex of *P. discolor* represent IR roughness as a rate code.

In addition to intracortical mechanisms underlying the generation of a rate code for high-modulation frequencies, a transformation of the temporal code into a rate code at the level of the IC is also discussed (Langner, 1992). Hewitt & Meddis (1994) simulated the transformation of a temporal code for amplitude modulation in cochlear-nucleus sustained-chopper cells into a rate code of amplitude modulation through inferior-colliculus coincidence-detector cells. Ongoing experiments in our lab try to localize the neural substrate for the transformation of roughness into a rate code.

Although the auditory cortex may simply reflect properties of periodicity coding generated in the midbrain, the auditory cortex is crucial for relating an auditory representation to behavior (Heffner & Heffner, 1990; Riquimaroux et al., 1991; Smith et al., 2004). It has been suggested that the role of the auditory cortex might be to organize sound features already extracted by lower levels into auditory objects (Nelken, 2004). Previous work indicates that for *P. discolor*, the IR roughness contributes to auditory object formation (Grunwald et al., 2004). Thus, the neural correlate of psychophysical performance for auditory object identification is most likely to be found in the auditory cortex.

The current comparison of the psychophysical and neuronal performance was based on the pooled responses of all 14 roughness-sensitive units. The response of no single unit on its own matched the psychophysical performance. To investigate the least number of units required to match the psychophysical performance, we repeated the ROC analysis for subsets of the roughness-sensitive units. The ideal-observer results are shown together with the psychophysical performance in Figure 1.8. With a lower number of units included for the ROC analysis, the ideal-observer performance drops remarkably. Note that the repeated random drawings of a subset of the 14 roughness-sensitive units resulted in quite stable predictions of ideal-observer performance. This finding confirms that this small population of 14 units is in itself homogeneous.

It is highly likely that there are many more roughness-sensitive units in the auditory cortex of *P. discolor*. Thus, it must be assumed that the animal's ability to combine the neural information across units is suboptimal.
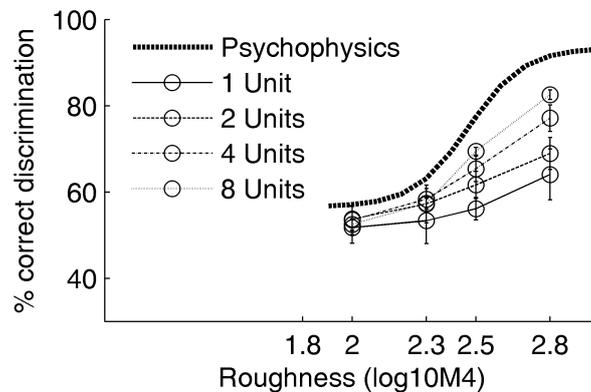
Figure 1.8: Ideal-observer performance for roughness discrimination as a function of the number of pooled unit responses. The strong dotted line shows the psychophysical performance replotted from Figure 1.4. The ideal-observer responses were obtained by 10 random draws of the specified numbers of units from the set of the 14 roughness-sensitive units. The error bars show SE across these 10 draws. With increasing number of pooled unit responses, the performance improves.

Although the current data show a high correlation between the psychophysical performance and the performance of a subpopulation of cortical neurons, this correlation does not prove a causal connection between the two. To this end, additional experiments should be performed in which the regions containing this subpopulation of roughness-sensitive neurons should be reversibly inactivated while the animals perform the psychophysical task. Nevertheless, the current results show that psychophysical sensitivity to IR roughness as an ecologically meaningful parameter is quantitatively encoded in the auditory cortex of the echolocating bat *P. discolor*.

1.6 Acknowledgements

2 Perception of ramped and damped complex echoes in the bat *Phyllostomus discolor*

2.1 Introduction

The results described in the previous chapter provide first findings about the roughness sensitivity of *Phyllostomus discolor*. However, the applied procedure for generating the employed impulse responses resulted in unmodulated stimuli, which would correspond to an echolocation call and a following echo that completely permeate the foliage without attenuation. In a natural environment, this is highly unlikely. Theoretically, two different general shapes of natural impulse responses are imaginable. First, a bush could have a couple of small leaves or twigs sticking out of the general foliage, resulting in an impulse response with several small reflections in the short delays, followed by reflections with increasing number and amplitude. Thus, this type of impulse response receives a ramped envelope modulation. Second, a tree's impulse responses could just be attenuated with increasing foliage penetration, resulting in an impulse response with damped envelope modulation. Figure 2.1 illustrates these two cases.

A few years ago, Wolfram-Peter Stilz undertook an extensive study to investigate the acoustical reflection properties allowing the classification of horizontal and vertical backgrounds (Stilz, 2004). In doing so, he also recorded the echoes of several different trees and bushes. Indeed, the resulting sonagrams showed mostly echoes with a damped envelope structure, but also some with a ramped envelope.

The question now arising is: do these envelope modulations have an impact on the bats' roughness discrimination performance, and if so, which one? Patterson conducted studies on different pure tones with a ramped or damped envelope modulation, in which human listeners had to decide which of the two envelope modulated pure tones sounded more like an sinusoid (Patterson, 1994a,b). Akeroyd & Patterson (1995) repeated the experiment with envelope-modulated white noise instead of pure tones, the
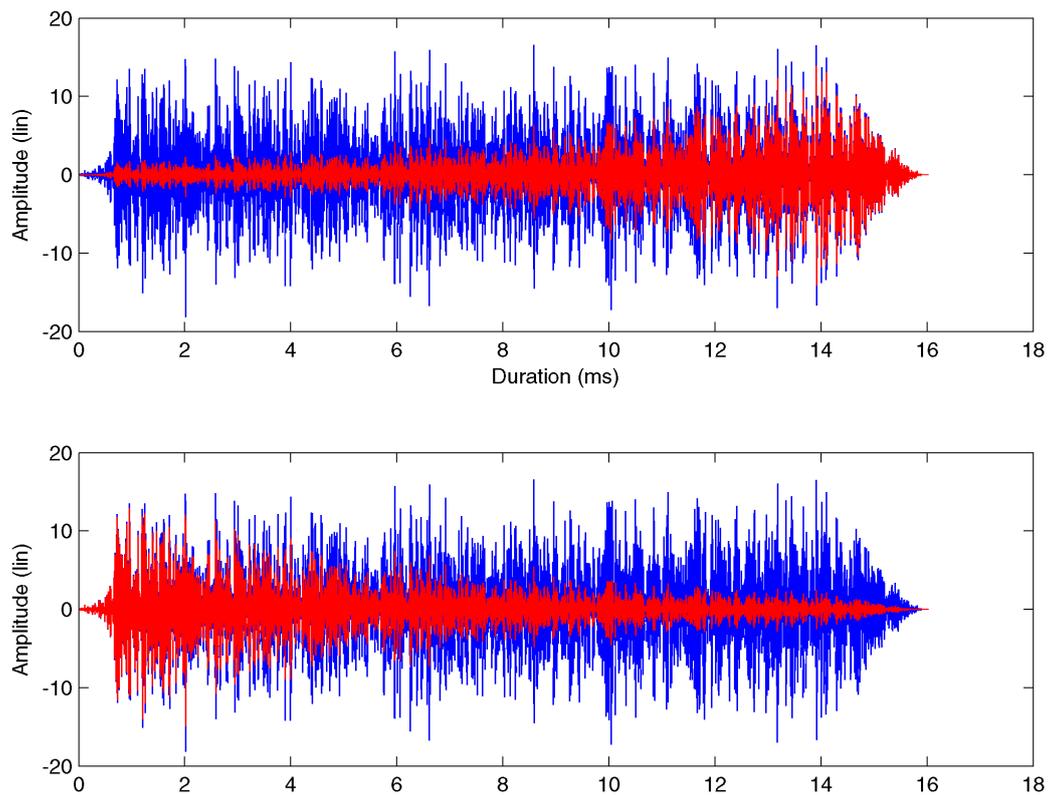
Figure 2.1: Example of impulse responses with a ramped and a damped envelope modulation. The basic impulse response is in both cases identical (shown in blue). Above, the basic impulse response is superimposed by the same impulse response whose envelope has been modulated to increase by 20 dB over time. Below, the same was done, only this time with an inverted envelope modulation so that it decreases by 20 dB over time.

listeners here had to decide for the signal with the typical hiss quality normally associated with noise. In all studies, the listeners clearly preferred the signal with the ramped envelope modulation, which means that this modulation variant seems to leave the original sound quality more intact. However, it is unknown if this is also true for the statistical signal properties, like the roughness.

It could be hypothesized, that a ramped envelope modulation could lower the discrimination threshold determined in the last chapter because of smaller masking effects. When observing a complex impulse response like the ones used in the preceding experiment (compare figure 0.2, left example, p. 5), it is conceivable that some of the single reflections, especially the ones with a high amplitude, could mask the following reflections. This is called Forward Masking (Moore, 2003). Because of the now ramped envelope structure, the following reflections on average possess a higher amplitude than the preceding reflections, causing a subsidence of the masking effect. This could give the bat access to more information concerning the impulse response's roughness, therefore lowering the roughness discrimination threshold.

It is also conceivable that a damped envelope modulation would increase the forward masking effects, therefore also increasing the roughness discrimination threshold measured in the original experiment.

Based on this, the experiment described in the previous chapter was repeated, only this time with stimuli that possess either a ramped or damped envelope modulation. The fixed reference roughness used was 1.8 (log10M4). This allowed testing if the minimal roughness of 2.5 (log10M4), that had been determined to be necessary for reliable roughness discrimination (see section 1.4.1, p. 16), is affected by the envelope modulation.

2.2 Methods

2.2.1 Animals

The animals used for this study were the same as in the previous chapter (see section 1.3.1, on page 11). As the time span between the completion of the previous experiment's data acquisition and the begin of this experiment was 13 months and all four bats were in the meantime involved in the training for a different experiment (Chapter 3), all bats had to be retrained for the task. For three of the bats, this took less than two weeks, the fourth was for unknown reasons not able to relearn the task in a stable manner.
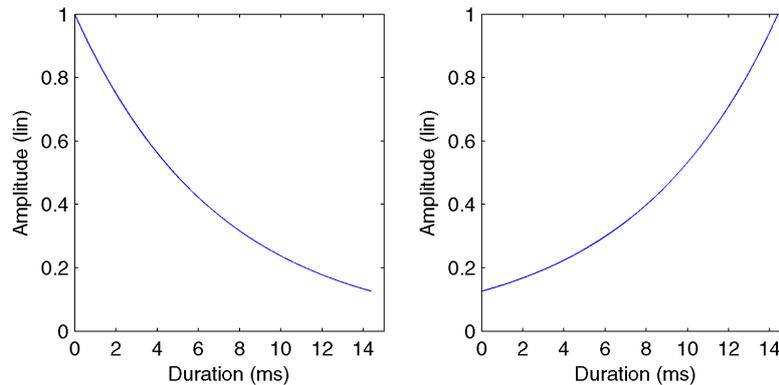
Figure 2.2: Illustration of the modulator-impulse responses used to generate the damped (left) and ramped (right) envelope structure of the test stimuli.

As the retraining and successive data acquisition of each bat began one week after its completion of the preceding experiment (see chapter 3), there was a difference in the training's starting point of up to 3 months. Therefore, the bats completed this experiment almost consecutively.

2.2.2 Impulse responses

The basic pool of test-impulse responses used in this experiment consists of the 775 impulse responses described in the previous chapter (1.3.2, p. 11). A modulator-IR with a size identical to the test-IRs (3597 samples) was generated with an amplitude that decreased linearly by 20 dB from begin to end. Prior to each trial, each tested IR was modulated with either this modulator-IR (for a damped test condition) or the inverted variant (for a ramped test condition, see figure 2.2).

The resulting, envelope-modulated test stimuli are depicted in figure 2.3, rows 1 & 3. To illustrate how the actual echo received by the bats during the experiment, might look, a recorded echolocation call of *P. discolor* was convolved with the depicted example impulse responses (rows 2 & 4). The bottom row shows the magnitude spectra of the ramped and damped artificial echoes in the rows 2 & 4, which are more or less identical.

2.2.3 Experimental setup

The setup was identical to that described in the previous chapter (cp. section 1.3.2.2, p. 14).
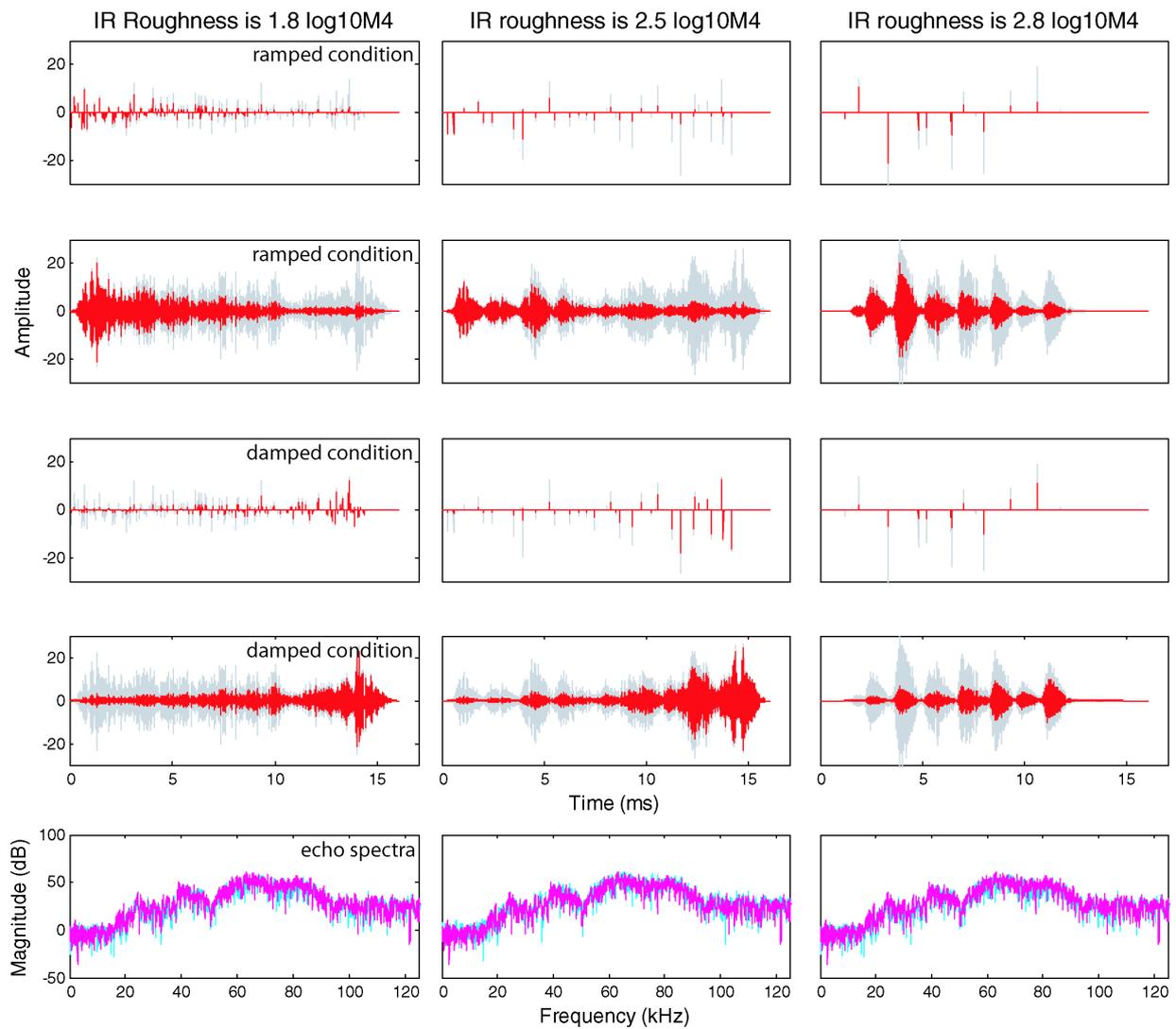
Figure 2.3: Examples for three complex IRs with different roughnesses (left to right: 1.8, 2.5 and 2.8 (log10M4)). Top row: the damped condition shown in red (cp. the unmodulated condition in grey). The second row shows the same IR, but convolved with an recorded *P. discolor* echolocation call. The third and fourth rows show IR and convolved IR for the ramped condition. The fifth row shows the echo spectra for ramped (cyan) and damped (magenta) condition.

2.2.4 Procedure

The basic procedure in this experiment was also identical to that described in the previous chapter (page 14). The differences are that for one thing, the reference-IR always had a roughness of 1.8 (log10M4). Furthermore, both the reference-IR and the test-IR possessed either a ramped or a damped envelope modulation.

For the training and the data acquisition of the first bat (Blanche), just one envelope modulation type - first damped, then ramped - was used until the data acquisition was completed for this condition. Afterwards, data acquisition began anew for the ramped envelope modulation. For bat two and three (Rose and Sophia), this was handled differently. Here, alternations between the ramped and the damped condition were conducted on a daily basis, i.e., on one day only the ramped condition, on the other only the damped. This was done to make sure that the animals didn't grow too accustomed to one condition, and to see if there is a difference in the results for these two procedures.

2.3 Results

Again, a psychometric function was generated for each bat and each envelope condition, based on 30 trials per condition. Figure 2.4 shows the results for the three bats as a function of the test-IR's roughness. The thresholds for the ramped condition ranged between 2.26 and 2.39 (log10M4), the thresholds for the damped condition ranged between 2.38 and 2.43 (log10M4). All the thresholds for both conditions therefore were below the measured threshold of 2.5 (log10M4) for unmodulated IRs. For two of the bats (Rose and Blanche), the threshold for the ramped condition was below the threshold for the damped condition. For the remaining bat (Sophia), the thresholds were practically identical. The mean threshold for the ramped condition was 2.34 (log10M4), for the damped condition 2.40 (log10M4). According to a statistical analysis (paired t-test, $p<0.05$), the null-hypothesis (the thresholds of one condition do not differ from the thresholds in the other condition) cannot be rejected, which means that the bats' performances for the ramped and damped conditions are not statistically different.
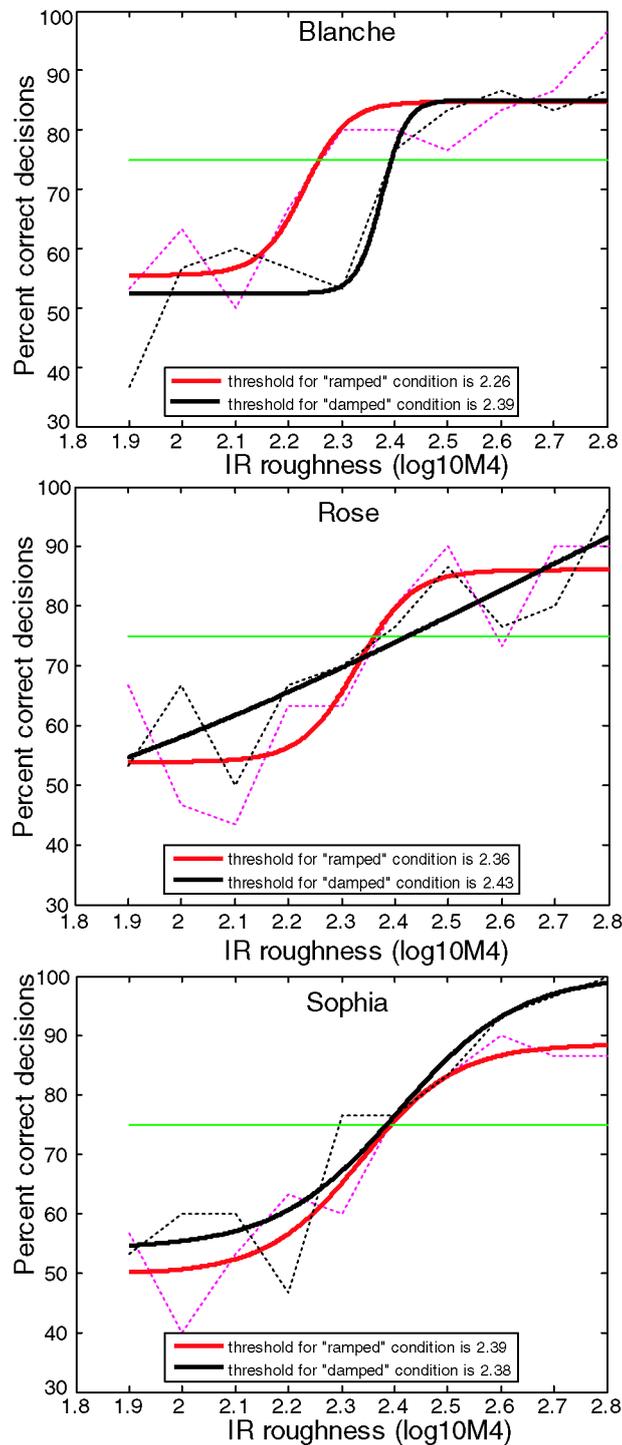
Figure 2.4: Results for both envelope conditions for all three bats. The dotted lines represent the actual performance of each bat for either ramped (black) or damped (magenta) condition. The solid lines illustrate a sigmoid fit for each psychometric function.

2.4 Discussion

This experiment investigated the effects of different envelope modulations on the echo-roughness discrimination ability of *P. discolor*. When using artificial echoes based on unmodulated IRs, the minimal roughness necessary for reliable discrimination of two IRs is 2.5 (log10M4) (cp. previous chapter, section 1.4.1 on page 16). But, according to a study by Stilz (2004), natural echoes possess either an increasing (ramped) or decreasing (damped) envelope structure.

In the previous chapter, we stated that neurons sensitive to the envelope-modulation-depth of the stimuli could be responsible for the bat's roughness sensitivity (cp. previous chapter, section 1.5, p. 23). In order to be able to evaluate the stimulus' envelope-depth, the bat preferably has to have access to the complete stimulus. As it can be presumed that the damped envelope modulation considerably increases these masking effects, the bat's access to the envelope-depth will diminish, therefore explaining the higher discrimination threshold compared to the ramped envelope modulation. This ramped envelope modulation on the other hand could in this case lessen the masking effect and thereby improve the bat's access to the signal's envelope modulation.

According to the results, this did not prove to be true. For one of the bats (Sophia), the performance for the two conditions was more or less identical. The other two bats only showed a very small difference in their discrimination thresholds, although the threshold for damped IRs was always somewhat higher than for the ramped. A statistical evaluation confirmed that at least these three bats do not discriminate ramped and damped IRs with a significant difference.

What attracts the attention, though, is that the thresholds of all three bats for both ramped *and* damped envelope modulations are *below* the 2.5 (log10M4) threshold measured with unmodulated IRs (cp. previous chapter, section 1.4.1, p. 16). Following our hypothesis as stated above, we expected the ramped threshold being below the unmodulated one, and the damped threshold above. The explanation for the differing result can be found by re-evaluating the roughness of the modulated IRs. Both envelope modulation types change the IRs roughness by increasing the roughness by an amount of approximately 0.2 (log10M4). Yet, the roughness specifications given in the x-axes of the results, on which the determined thresholds are also based, refer to the roughness that the original unmodulated IRs possessed. So, 0.2 has to be added to all found discrimination thresholds. This also means that the roughness of the reference IR was not 1.8, as intended, but 2.0 (log10M4). However, since the results in the previous chapter

indicated that for *P. discolor*, roughnesses below 2.5 (log10m4) are indistinguishable (see figure 1.2, p. 17), the change in the reference roughness should have had no repercussions. For the discrimination thresholds, the roughness adjustments effectuate corrected thresholds of 2.6 (log10M4) for the bat Sophia. For the other two bats, the new thresholds are 2.46 respectively 2.56 (log10M4) for the ramped condition and 2.59 respectively 2.63 (log10M4) for the damped condition. From this follows that both conditions effect no improvement in the discrimination performance of the bats, besides (statistically insignificant) cues for slightly higher threshold for the damped condition. This suggests that the necessary roughness-information content that is needed by the bats for their discrimination task is gathered by them from the echoes in a way that is not affected in any way by both envelope-modulation types. Repetitions of this experiment with additional bats would presumably further clarify this, but were not conducted yet.

2.4.1 Comparison of psychophysical and neurophysiological data

In the previous chapter, a parallel neurophysiological study, undertaken by Uwe Firzlaff and Susanne Hoffmann, used the same unmodulated IRs that were applied in the behavioral study to search for roughness-sensitive neurons in the auditory cortex of *P. discolor*. It could be shown that a pool of 14 roughness-sensitive cortical units was sufficient to perform the roughness discrimination task with an almost identical performance (see figure 1.6, p. 22).

For the envelope-modulated IRs used in this study, again a neurophysiological study was conducted in our lab. Frank Borina investigated roughness-sensitive neurons in the inferior colliculus (IC) of *P. discolor*, using unmodulated as well as envelope modulated IRs (both ramped and damped, publication in prep). Based on his data and the results of this study, we compared the behavioral with the neurophysiological performance by again employing the ROC-procedure as described in the previous chapter (cp. 1.4.3, p. 21) to generate a neurometric curve that can be compared with the psychometric curve of the behavioral data.

This neurometric curve is based on 29 roughness encoding units in the IC of *P. discolor*. Although the psychometric and the neurometric curves are similar and also produce similar discrimination thresholds for the ramped condition, the curves don't agree as well as in the example with the auditory cortex-units and the unmodulated IRs (illustrated in the previous chapter, figure 1.6, p. 22), even though that neurometric curve was based on only 14 units in the auditory cortex. However, as figure 1.8 (p. 27) in the
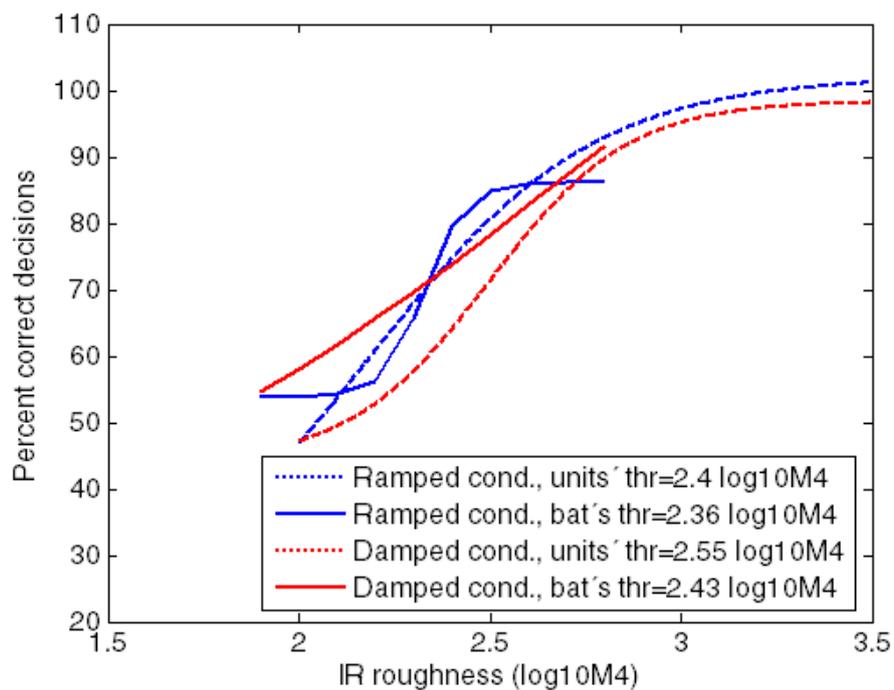
Figure 2.5: Comparison of psychoacoustical and neurophysiological results. The solid curves illustrate the psychometric data of the bat "Rose", the dotted curves illustrate the neurometric data calculated by using a ROC-analysis of the neurophysiological data gathered by Frank Borina (see text). Data referring to the ramped envelope modulation is depicted in blue, the damped condition in red.

previous chapter shows, the performance of the ideal-observer based on the responses of the roughness-sensitive units in the auditory cortex declines rapidly with a decreasing number of units. Only with all 14 units available is the ideal observer performance comparable with the psychophysical performance.

Therefore, one reason why the present psychophysical/neurophysiological comparison only shows a rather poor match could be that the number of the employed IC-units wasn't large enough to solve the discrimination task with a result comparable with psychophysical performance. Another possible explanation is that these IC-units constitute only one of the neural components necessary for roughness discrimination. As already mentioned in the previous chapter, it has been suggested by Israel Nelken (2004) that up to the level of the IC, most of the auditory features from incoming sounds are in fact already extracted, but not fully transformed and organized into a neural representation of the auditory object until the level of the auditory cortex. Therefore, it is conceivable that the roughness encoding units found so far by Frank Borina contribute an important part regarding the roughness discrimination, which needs to be completed by other, momentarily still unknown factors.

2.4.2 Regarding our findings in a biological context

An open question is if the roughness discriminating capability of *P. discolor*, as measured in our virtual object experiments, is indeed sufficient to also discriminate and classify real objects in the bat's natural habitat. Unfortunately, there are, to our knowledge, no surveys of the echo-acoustic features of the neotropical vegetation available. The only alternative is represented by the aforementioned study of Wolfram-Peter Stilz (2004), which focuses exclusively on local natural objects, though.

Comparing Stilz' data with ours turned out to be rather complicated, however. For example, in Stilz' study, the position of the ensonifying device compared to the ensonified tree was fixed at a distance of 1.5 m. Combined with the cone-shaped sound propagation of this device (30° solid angle), this means that the roughness of the resulting echo is not only influenced by the permeation depth of the ultrasonic signal, but also by the ensonified surface of the tree. The bigger the ensonified surface, the more reflecting surfaces will be at the echo's onset. Although it is clear that the amplitudes of the individual reflections depend of the reflecting surface's size, it is at the moment unknown how exactly the dimensions of the ensonified area are encoded in the echo. We can therefore neither duplicate the conditions of Stilz' study in our experiments, nor deter-

mine the exact dimensions encoded in our computer-generated IRs. It could therefore theoretically be that the IRs that we present to the bats represent sections of the virtual targets that are smaller or larger than the ensonified sections of the trees in Stilz' study, therefore improving or worsening the information content of the resulting echoes.

Further on, comparing Stilz' determined roughness values with our data required the setting of a common basis of computation for the respective roughness measurements. With the willing support of Wolfram-Peter Stilz, this posed no problem. All of the following roughness values taken from his study were converted to our mode of calculation. Also, as most of the recorded echoes depicted in his study feature damped envelopes, all of our IRs that were used for the following comparisons had a damped envelope modulation.

According to Stilz' study, the echo-roughnesses of the trees he investigated ranged from 0.7 to 2.2 (log10M4). The corresponding IR-roughnesses ranged from 1.0 to 1.8 (log10M4). As this is below the discrimination threshold of 2.5 (log10M4) determined in the previous chapter, this suggests that roughness-based discrimination of these trees by *P. discolor* would not be possible. However, there are several factors concerning these results that warrant further consideration.

First, let us take a closer look on the IRs. In his study, Stilz obtained his IRs by ensonifying the actual plants with an artificial, bat-call like ultrasonic signal (linear downward sweep from 140 to 20 kHz, 4 ms duration). The resulting echo contained the ensonified plant's IR, but only defined for the frequency-spectrum of the applied ensonification-signal. These embedded IRs were extracted by a cross-correlation of the ensonification-signal and the echo and will be termed cross-correlated IRs (xIRs) from now on. Although this cross-correlation method is absolutely correct, it does not produce the complete IR, due to the spectral limitations of the applied ensonification-signal. The xIR is therefore only defined for the spectral content of the ensonification signal. In order to gain the complete IR, one has to use an approximate dirac impulse, which is technically very challenging.

In contrast, as we generated our - artificial - IRs ourselves, we had the full information available for all calculations from the start. Hence, to adjust our IRs for better comparison with Stilz' xIRs, we re-evaluated the roughness of our IRs by first convolving them with a recording of the ensonification-signal used by Stilz, which he kindly provided. We then zero-padded the resulting echo to a length of 40 ms, according to the echo duration recorded by Stilz, and cross-correlated this echo and the ensonification-signal. The

emerged xIRs now had roughnesses ranging from 1.3 to 2.4 (log10M4), therefore being not only considerably smoother than the roughness values of the original IRs, but also closer to those measured by Stilz. In our experiments, the IRs had to have a minimal roughness of 2.5 (2.6 for the corrected damped-condition roughness) in order to be discriminated by the bats. The xIR-equivalent to an IR with a roughness of 2.5 (2.6) has a roughness of 1.7 (all quantified as log10M4). This means that at least some of the local plants investigated by Stilz could indeed be discriminated by *P. discolor* based on their echo roughness. Figure 2.6 illustrates the different roughness ranges.
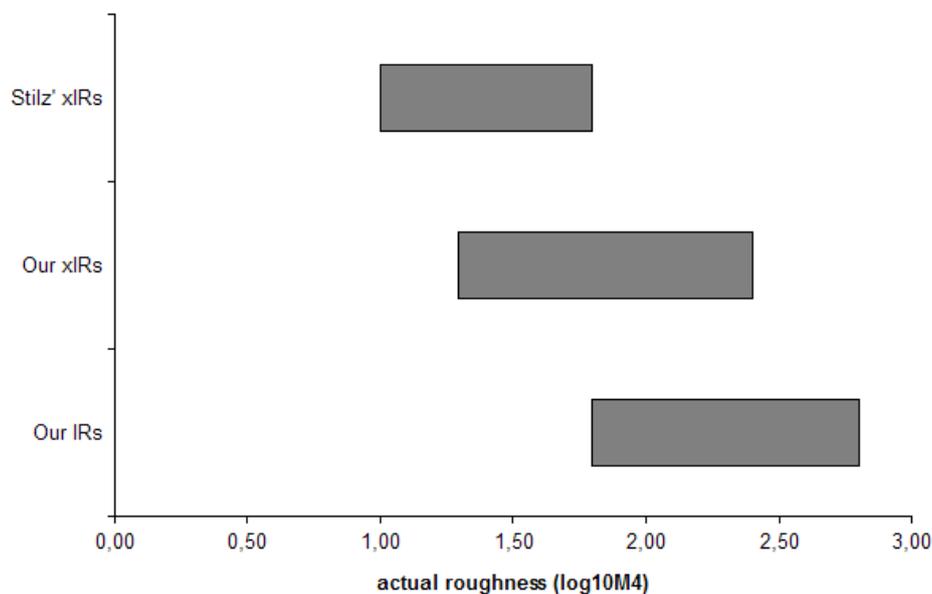
Figure 2.6: Comparison of the different roughness ranges of the xIRs determined by Stilz (2004) and us. The roughnesses of the respective xIRs intersect from 1.3 to 1.8 (log10M4). The lowest bar represents our original IRs, which have no counterpart in Stilz' study.

Of course, this assumes that the bats are indeed able to extract the xIR from the echo. Although there are, as mentioned in the general introduction, some indications that this is in fact the case (Weissenbacher & Wiegrebe, 2003), there have been no studies yet regarding echoes with the complexity and duration comparable to those at hand. So, we also have to consider the roughness information of the echoes themselves, as they are perceived by the bats. We therefore again generated artificial echoes, this time by convolving our damped IRs with a recorded echolocation call of *P. discolor*. These echoes possess a roughness between 1.0 and 1.6 (log10M4). This range is completely covered by the echo roughnesses as determined by Stilz (0.7 to 2.2 (log10M4), figure 2.7).
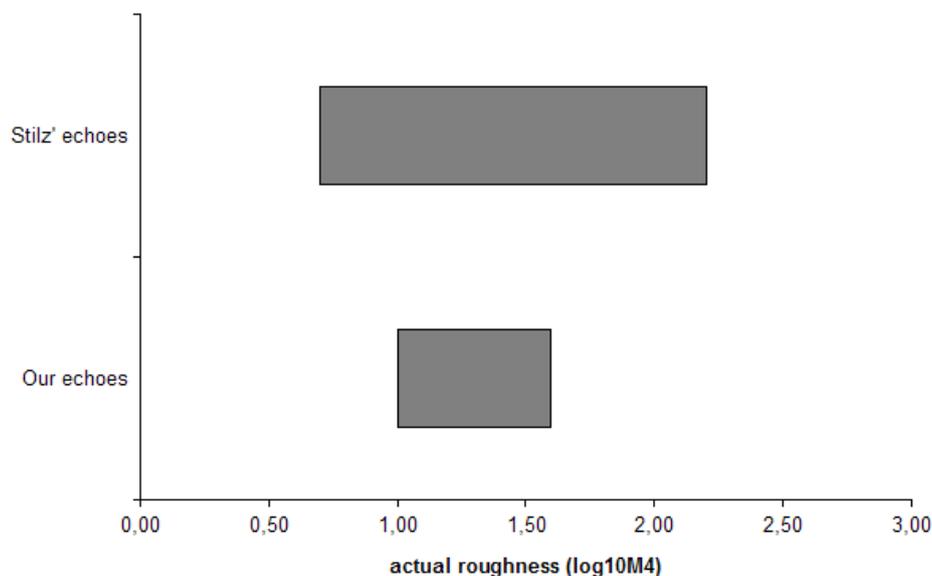
Figure 2.7: Comparison of the different roughness ranges of the echoes determined by Stilz and us. The echoes generated from our IRs, using a recorded call of *P. discolor*, feature a roughness range completely covered by the roughnesses of local trees as determined by Stilz.

The broader roughness-range of Stilz' echoes can presumably be explained by the fact that the IRs underlying our artificial echoes all possess the same linearly damped envelope, which means that this characteristic is also present in the resulting echoes. It can be assumed that the envelope of the genuine echoes recorded by Stilz, although also having a damped shape, differ in their respective degree of attenuation over time, resulting in a multitude of differently damped echoes and therefore a broader roughness-range.

Also, the respective echoes (that is, those obtained by Stilz and the artificial echoes generated by us) are based on different ensonification signals. While we used a recorded, but authentic echolocation call of *P. discolor* (figure 2.8, right spectrogram), the ensonification signal used by Stilz was a completely artificial sweep. Although the sweep's parameters (frequency range 140-20 kHz, duration 4 ms) were chosen to resemble an echolocation call of a local *Myotis*-species, it lacked the multi-harmonic structure appertaining to the echolocation-calls of these bats (figure 2.8, left spectrogram) which could also influence the emerging echo's roughness.

Apart from that, one has to keep in mind that naturally, Stilz' study cannot provide any information about the echo-acoustic properties of the actual habitat of *P. discolor*, the neotropical forest. When regarding the typical vegetation in the neotropical rainforest
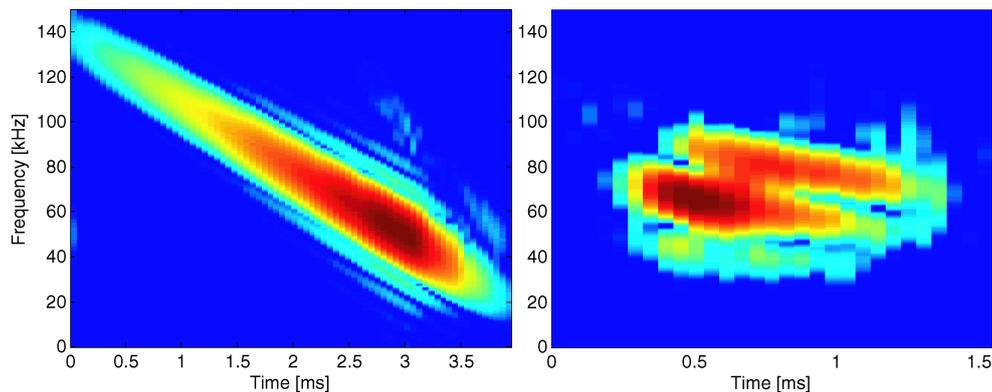
Figure 2.8: Spectrograms of the ensonification signal used by Stilz (left) and the echolocation call of *P.discolor* (right. Note the multi-harmonic structure in the echolocation call. In the upper right corner of the left spectrogram, a harmonic of the signal is visible, but only very faint and has therefore most likely no perceptible influence.

compared to the local vegetation (figure 2.9), it seems like if the neotropical vegetation is to some extent composed of bigger leafed plants, which would, according to Müller & Kuc (2000), result in a higher roughness than featured by the local variants. This could mean that the echo-roughnesses encountered by *P. discolor* in its natural habitat are in the range that allows the bat to discriminate them. Actual data on the echo-acoustic properties of the neotropical vegetation, comparable to Stilz' study, is in dire need to confirm this, but sadly not available yet.

Because of all these issues, the comparisons of Stilz' data and ours can only be evaluated qualitatively, and not really quantitatively. Still, they allow for a first impression about the implication of roughness-sensitivity in bat sonar for the orientation in a bat's natural habitat, and therefore shouldn't be disregarded.

Which questions remain? It is still unclear if the minimal roughness discrimination difference assessed in the last chapter (min. 0.3 (log10M4)) for unmodulated signals above 2.5 (log10M4) is still valid for the envelope-modulated signals. It could very well be that this value also stayed constant. However, experiments concerning this haven't been conducted yet.

To conclude: we have shown that the bat *P. discolor* is still able to perform roughness-based echo discrimination when the employed impulse responses have a more natural shape. The envelope modulations don't seem to affect the discrimination performance in any way, as the discrimination threshold stays all but constant. Qualitative compar-

isons with data concerning the echo-roughness of real trees suggest that a roughness-based discrimination of natural vegetation is indeed feasible.

(a) *Typical local vegetation*

(b) Rainforest in Costa Rica

Figure 2.9: a) Photographs of an apple tree, a spruce, a copper beech and a sloe, taken from Stilz (2004) b) Photograph of the rain forest in Costa Rica.

3 Phase sensitivity in bat sonar revisited

3.1 Abstract

Whenever a bat echolocates, the generated echo consists of the convolution of the echolocation call and the impulse response (IR) of the ensonified object. A crucial question in animal sonar is whether bats are able to extract this IR from the echo. The bat inner ear generates a frequency representation of call and echo and IR extraction in the frequency domain requires accurate analysis of both magnitude and phase information. Previous studies investigating the phase sensitivity of bats using a jitter paradigm reported a temporal acuity down to 10 nanoseconds, suggesting perfect sonar phase representation. In a phantom-target playback experiment, we investigate the perceptual phase sensitivity of the bat *Phyllostomus discolor* using a novel approach: instead of manipulating IR phase by changing IR delay, as it is done in a jitter paradigm, we randomized IR phase and thus lengthened the IR over time, leaving the magnitude spectrum unchanged. Our results show that phase sensitivity, as reflected in the analysis of signal duration, appears to be much lower than phase sensitivity, as reflected in the analysis of signal onset. The current data indicate that different temporal aspects of sonar processing are encoded with very different temporal resolution and thus an overall claim of 'phase sensitivity' as such cannot be maintained.

3.2 Introduction

Echolocation enables bats not only to find their way in absolute darkness, but, by comparison of echolocation call and echo, it also allows them to gain information on a multitude of parameters about the ensonified objects, like object distance, size, and shape.

The echo consists of the bat's echolocation call convolved with the ensonified object's impulse response (IR). The IR can be seen as the acoustic image of an object. The IR of an object corresponds to the sum of the reflections when the object is ensonified with a Dirac impulse (an impulse with a theoretically indefinite frequency range and an indefinite shortness). As a bat's echolocation call is usually several milliseconds long and only covers a certain frequency range (45-90 kHz in *Phyllostomus discolor*), the echo is not the IR itself, but the IR imprinted on the echolocation call. For several decades now, there has been an ongoing discussion about whether bats are able to extract an object's IR from the perceived echo. Note that the echo, unlike the IR, contains the acoustic features of both the emitted call and the object's IR. Thus the IR, extracted through a detailed comparison of call and echo, would give the bats better access to the above-mentioned object parameters. In theory, IR extraction is possible either in the time domain by cross-correlation of the echolocation call and the inverted echo waveform, or alternatively in the frequency domain, where the same is achieved by multiplying the magnitude spectra of call and echo and adding the phase spectra. As in the bats auditory periphery, the temporal representations of call and echo are at least partially converted into the frequency domain, as preservation of phase information is mandatory for subsequent auditory IR extraction. There have been many studies investigating the phase sensitivity of bats (Menne et al., 1989; Moss & Schnitzler, 1989; Moss & Simmons, 1993; Simmons, 1979; Simmons et al., 1990a). All of these studies used a jitter target paradigm, i.e. the bats had to discriminate an echo with a static delay from an echo with a delay that jitters back and forth over a given range. Simmons et al. (1990a) found that the minimal jitter that can be detected by the bat *Eptesicus fuscus* is as low as 10 ns. However, both result and paradigm have been the topic of a controversial debate for several years now (Beedholm, 2006; Beedholm & Mohl, 1998; Pollak, 1993; Simmons, 1993; Simmons et al., 2003). In this study, we took a different approach to quantify phase sensitivity of bat sonar. Instead of changing the IR phase spectrum by changing the echo delay, we changed the phase spectrum by changing echo duration. Note that both delay and duration are encoded exclusively in the phase spectrum of a sound. Here we quantify perceptual sensitivity to sonar phase in a phantom-target, playback experiment by measuring the minimal increase in echo duration required for the bats to discriminate a lengthened echo of their call from a simple, perfect reflection of their call. This measure of sonar phase sensitivity is independent of the hitherto used jitter paradigms.

3.3 Methods

3.3.1 Animals

Four female bats of the neotropical species *Phyllostomus discolor* were used for this experiment. *P. discolor* emits broadband multi-harmonic echolocation calls covering the frequency range between 45 and 90 kHz. The predominant diet of *P. discolor* consists of fruit, pollen and nectar (Rother & Schmidt, 1982). All four animals were housed together with free access to water except during individual training sessions. Training sessions were usually conducted on five days each week, followed by a two-day break. On training days, the bats received food only as a reward (consisting of banana-pulp) in the training setup. On the days without training they received mealworms (larvae of *Tenebrio molitor*).

3.3.2 Experimental Setup

The experiment was implemented as a virtual playback paradigm. The bats were required to evaluate the echoes of their echolocation calls, generated by a real-time convolution of their calls with the IRs described below. Training was conducted in a 2-alternative, forced-choice playback setup. It consisted of a Y-shaped maze, mounted inversely on the wall of an echo-attenuated chamber at an angle of 45 degrees. The starting position was located at the now upper end of the Y, and a reward feeder was mounted at the end of each of the two other ends. Additionally, a 1/4'''-ultrasonic microphone (Brüel & Kjaer Instruments 4135, Naerum, Denmark) and an ultrasonic speaker (Matsushita EAS10 TH800D, Osaka) were mounted at each of the lower ends facing toward the starting position. During the experiment, the emitted echolocation calls were recorded by both microphones, amplified (Brüel & Kjaer Instruments 2610) and band-pass filtered (30-100 kHz, Krohn Hite 3550, Brockton, MA), then digitized by one of two data-acquisition boards (Microstar DAP 5200a, Bellevue, WA) at a sampling rate of 250 kHz. On both sides, the recorded calls were convolved with different IRs. Convolution was done by zero-padding both the recorded call and the IRs to 1024 samples, multiplying the complex spectra of recorded call and IR, and inverse Fourier transformation. This procedure replicates the formation of the echo of a real object, i.e., every change in the bat's echolocation call results in an immediate change in the artificial echo. An implemented trigger made sure that active vocalization of the bat was mandatory to start the creation of the artificial echoes. The artificial echo was then am-
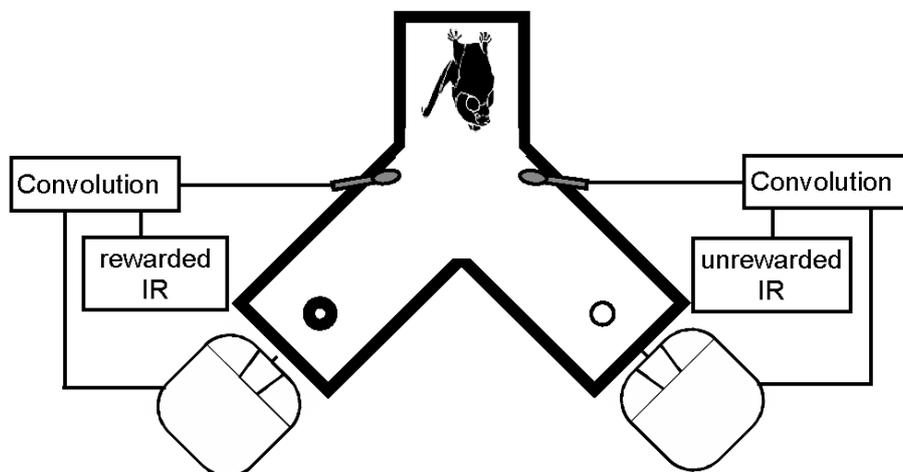
Figure 3.1: Setup schematic. The platform is wall mounted at an angle of 45°, the angle between the two legs is 90°. The two playback channels (each consisting of a microphone, measuring amplifier, bandpass filter, DAP board, amplifier, and a speaker) were independent of each other. Every echolocation call of the bat was recorded by both channels, convolved with a different IR for each channel (one a rewarded IR, the other an unrewarded, lengthened IR) and played back to the bat as an artificial echo. The bat then had to crawl toward the speaker from which the artificial echo containing the rewarded IR originated to receive a food reward.

plified (Harman/Kardon 6110) and played back to the bat after a total delay of 4.8 ms, corresponding to a target distance of 82 cm. The setup is illustrated in figure 3.1.

3.3.3 Stimuli

In a phantom-target experiment, bats do not evaluate presented sounds but echoes of their own vocalizations. The structure of the echo is defined by the IR with which the call is convolved to produce the echo. The rewarded IR consisted of a simple Dirac impulse. The convolution of an echolocation call with this IR produces an echo that is a delayed but otherwise identical version of the call. The unrewarded IR was designed to differ only in its phase spectrum from the rewarded IR. The unrewarded IR was generated by transforming the rewarded IR into the frequency domain with a Fourier transformation, randomizing the phase spectrum and inverting the Fourier transformation. The resulting IR is effectively a burst of white noise with the same magnitude spectrum as the rewarded IR but with a duration equal to that of the temporal window of the Fourier transformation. We used twelve different window durations of 8, 16, 32, 64, 128, 256, 512, 608, 712, 864, 1024, and 2048 μs. Convolution of an echolocation call with such a noisy IR results in an echo which is a delayed and lengthened version of the

call. The lengthening is equal to the Fourier-window duration minus 1 sample (4 μs). After equalization of the root-mean square IR amplitude, the IR level was roved over a range of ± 6 dB to prevent the bats from using echo loudness as a discrimination parameter. Furthermore, the delay of the click IR was randomized within the range of the phase-randomized IR duration to preclude the bats' use of echo delay as a perceptual cue. Examples of three rewarded and unrewarded IRs with unrewarded IR durations of 64, 256, and 1024 μs are shown in Fig 3.2. Superimposed on the IRs are echoes generated with these IRs and a recorded *P. discolor* echolocation call.

3.3.4 Procedure

All four bats were trained to discriminate two IRs in a two-alternative, forced-choice paradigm. To obtain a food reward, the bats had to learn to crawl towards the end of the leg where the echo generated with the impulse IR originated. As soon as the bats were able to discriminate the reward impulse IR from the unrewarded IR (with a duration of 2048 μs) with at least 85% proficiency, data acquisition started. The required time span for this training period varied for each animal and ranged between seven and twelve weeks. In every subsequent trial, both the rewarded and the unrewarded IR were generated anew, the latter according to a manually chosen Fourier-window duration. This manually chosen Fourier-window duration was kept constant for a block of five successive trials. Following a staircase procedure, the IRs used in the next block featured the nearest of the shorter Fourier-window durations mentioned above in order to facilitate the task learning for the bats. Both training and data acquisition took place five days a week for 20 minutes per day per animal. Each animal completed between 20 and 40 trials per training session. Psychometric functions, based on 30 trials per unrewarded IR duration, were obtained. The psychometric functions were fitted with a sigmoidal function. Discrimination threshold was set to 75% correct of the fitted function which, based on the 30 trials, corresponds to a significance level of p < 0.003. To check for long-term training effects, more than the necessary 30 trials per condition were obtained. When these effects indeed appeared, additional data acquisition sessions were conducted. Using a sliding 30-trial window, changes in the discrimination threshold were monitored until the performance of each animal was either stable or started to deteriorate (up to 120 trials for every condition). Figure 3.3 shows the development of the discrimination threshold for each bat. The performance thresholds reported here correspond to the 30-
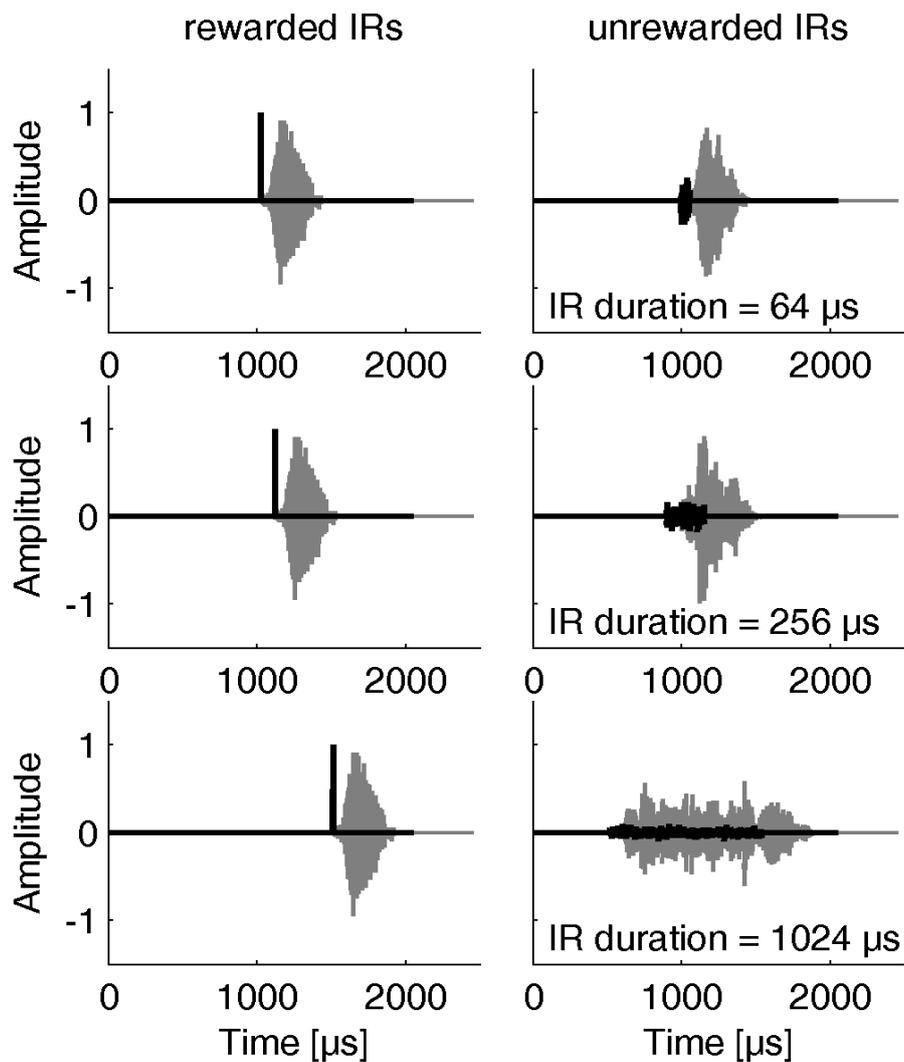
Figure 3.2: Illustration of the current phantom targets to investigate sonar phase sensitivity. The phantom targets are characterized by their IRs (black). The bats were trained to discriminate a rewarded impulse IR (left column) from an unrewarded noise IR (right column) sharing the same magnitude spectrum. Performance was assessed as a function of the unrewarded IR duration. Echoes generated with these IRs and a recorded *P. discolor* echolocation call are shown in grey.
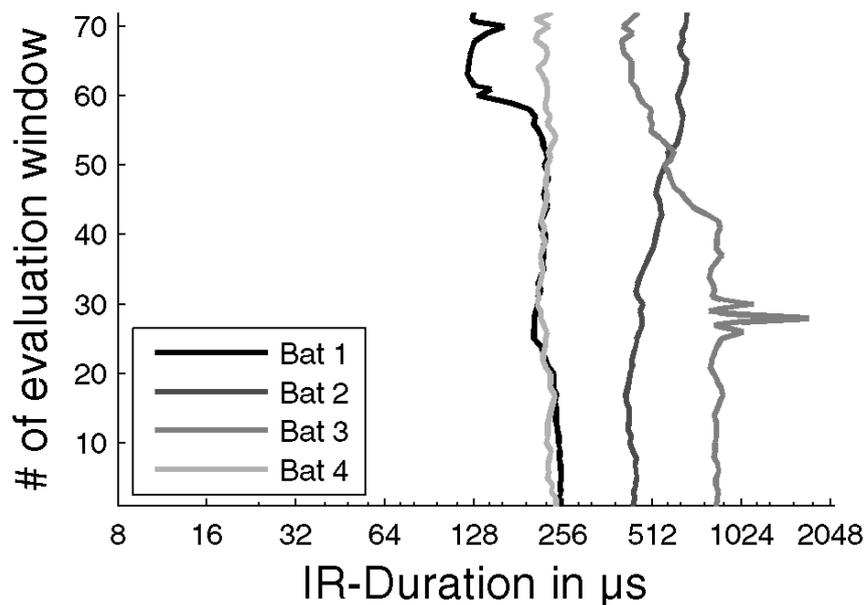
Figure 3.3: Development of the discrimination threshold for all bats. Each number on the y-axis represents one set of 30 trials per condition. For each subsequent set, the trials used were shifted by one step (trial #1-30 for the 1st set, trial #2-31 for the 2nd set etc.). For each of these sets, the respective discrimination threshold was determined. The four lines indicate the development of this threshold for every bat as a function of the trial set and therefore indirectly as a function of training time.

trial window with the best thresholds produced with this sliding analysis. The complete data acquisition took nine to thirteen weeks per animal.

3.4 Results

The current results are based on an overall of 5355 presentations of two phantom targets to four bats. Discrimination performance of the rewarded and unrewarded IRs is shown as a function of the duration of the unrewarded IR for the four bats in figure 3.4. Thresholds from these psychometric functions amount to 206, 372, 344, and 296 μs for bats one to four, respectively. The mean threshold is at 305 μs, with a standard error of ± 32 μs.
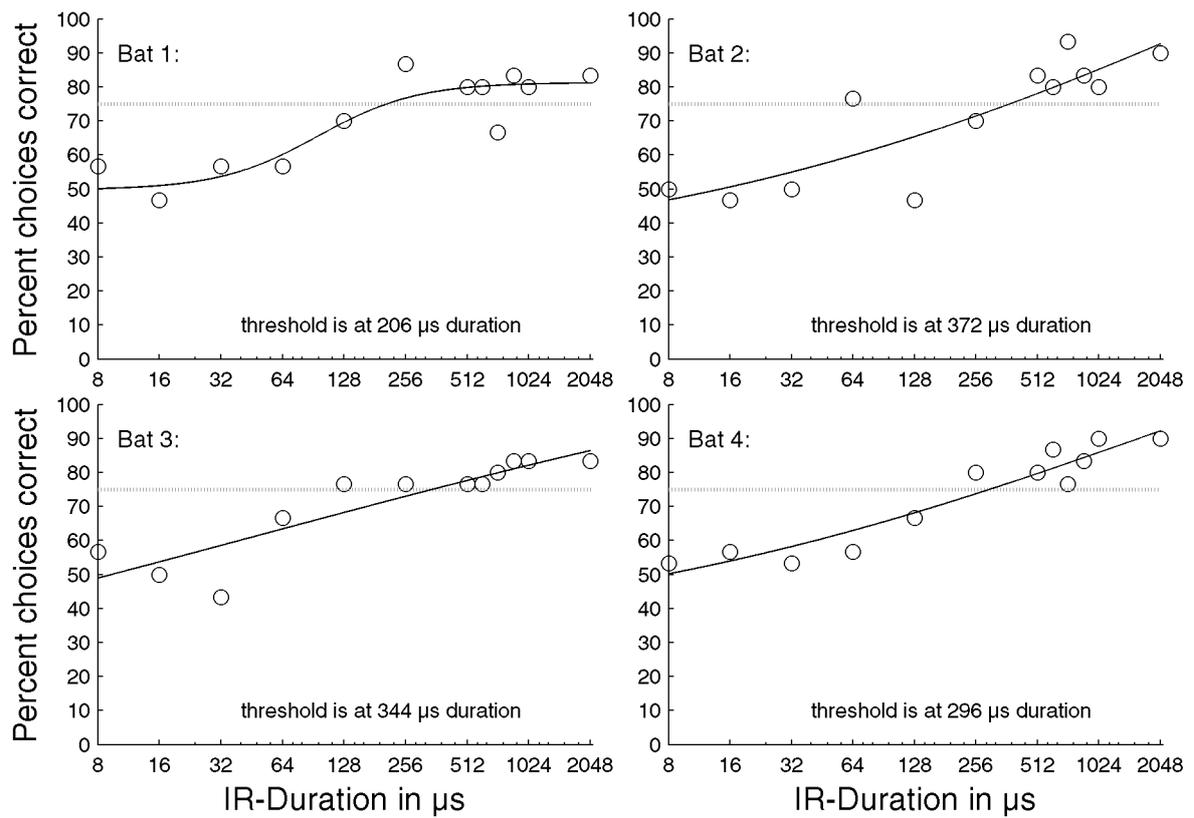
Figure 3.4: Performance of the bats in discriminating a rewarded Dirac-impulse IR from an unrewarded elongated IR. These IRs differ only in their phase spectra. Each open circle represents the performance for one of the unrewarded IR durations. The solid black line shows a sigmoidal fit to the performance data. The dashed line indicates the significance level of 75%. The threshold is defined as the point where the sigmoidal fit crosses the significance level.

3.5 Discussion

3.5.1 Difference between the jitter- and our paradigm

This study provides measures of sonar phase sensitivity of bats which are, contrary to hitherto existing studies (Menne et al., 1989; Moss & Simmons, 1993; Simmons, 1979; Simmons et al., 1990a, 2003), not based on a jitter paradigm. In the aforementioned studies, bats of the species *E. fuscus* were placed on a Y-shaped platform. In a two alternative, forced choice paradigm using two channels, the bat's echolocation calls were recorded by two microphones, one on each leg of the Y. Each call emitted by the bat was recorded by both microphones and the call's intensity impinging on each microphone compared, thereby determining towards which microphone the bat echolocates. The corresponding channel was then activated. If this happened to be the jittering target channel, the recorded echo was played back to the bat with a delay, which alternated between two consecutive echolocation calls by a specific delay difference. Decreasing this delay difference increased the difficulty for the bat to discriminate the jittering from the stationary target. According to these studies, the minimal delay difference that could still be discriminated by the bats was 10 ns (at a signal-to-noise ratio of 49 dB). This result caused much controversy due to possible flaws in the experimental design that could allow the bats to use unintended cues for their decisions thereby giving a different, less spectacular explanation for the 10 ns result (cf. (Pollak, 1993; Simmons, 1993) and (Beedholm, 2006; Beedholm & Mohl, 1998; Simmons et al., 2003)). Although Simmons et al. endeavored to compensate for these possible flaws (Simmons, 1993; Simmons et al., 2003), doubts concerning the result and the corresponding interpretation regarding the bats' full access to the signal's phase spectrum remained (Beedholm, 2006). This study used a fundamentally different paradigm. Here, we do not evaluate the bat's phase spectrum access by measuring its target range discrimination ability - or, in other terms, its sensitivity concerning IR onset - but instead the bat's sensitivity to IR duration. As the example of the Dirac-impulse and the white noise shows, IR duration is (like IR delay and every other temporal aspect of an acoustic signal) exclusively dependent on the IR's phase spectrum and can therefore be used as a measure of phase sensitivity. For four bats we determined the minimal IR duration necessary for each bat to be able to discriminate it from an IR consisting of a simple Dirac impulse. The resulting thresholds ranged from IR durations of 206 μs to 372 μs, with a mean of 305 μs (± 32 μs standard error).

3.5.2 Possible explanations for this discrepancy

This result indicates a limit in temporal sonar acuity that differs from that found by Simmons et al. by four orders of magnitude. In our view, this very large difference cannot be explained by the fact that the results were obtained from different bat species. While *E. fuscus* feeds exclusively on flying insects, *P. discolor* feeds mainly on fruit, but has also been reported to feed on insects depending on the habitat (Fleming et al., 1972; Willig et al., 1993). Species-specific differences in echo-acoustic acuity have been reported (Siemers & Schnitzler, 2004), but these differences do not by far reflect a discrepancy in the sensitivity to the relevant psychophysical parameter by four orders of magnitude. Another possible reason for the discrepancy of the current results from those obtained with the jitter paradigm may of course be the paradigm itself. As outlined in the introduction, both echo delay, as tested in the jitter paradigm, and echo duration, as tested in the current paradigm, are determined by the phase spectrum of the IR. It is conceivable, however, that these two echo-acoustic parameters probe very different limits of the bats auditory system. Specifically, for the jitter paradigm, stability of neural latency (Covey & Casseday, 1991) may play a crucial role whereas for echo duration, the sharpness of the temporal tuning of duration-sensitive units (Ehrlich et al., 1997; Gooler & Feng, 1992; Mora & Kossl, 2004; Penna et al., 2001) may be critical. In the ventral nucleus of the lateral lemniscus, stability of neural onset was found to be around 30 μs which is still three orders of magnitude higher than the behavioural accuracy of the delay-jitter experiments of Simmons et al. (1990a). Duration tuning on the other hand has not been studied for sounds shorter than about 1 ms. Thus, while a direct comparison of the behavioural data with these physiological results is only qualitative, it appears likely that a high sensitivity to echo delay cannot be interpreted as a high sensitivity to IR phase per se, as was suggested in Simmons et al. (1990a). If echolocating bats had access to the IR phase as it is defined in the phase spectrum, the bats should have been able to discriminate even the shortest possible randomization window of only 8 μs (2 samples at a sampling rate of 250 kHz, as used in our setup). One parameter that affects sensitivity to stimulus duration is the temporal integration associated with peripheral auditory filtering where the mechanical narrow-band filtering in the cochlea leads to a ringing response of the cochlea even when it is stimulated by a single impulse. Wittekindt et al. (2005) estimated the frequency selectivity of the *P. discolor* cochlea by measuring distortion-product otoacoustic emissions. An estimate of the associated temporal integration can be obtained by fitting the transfer function
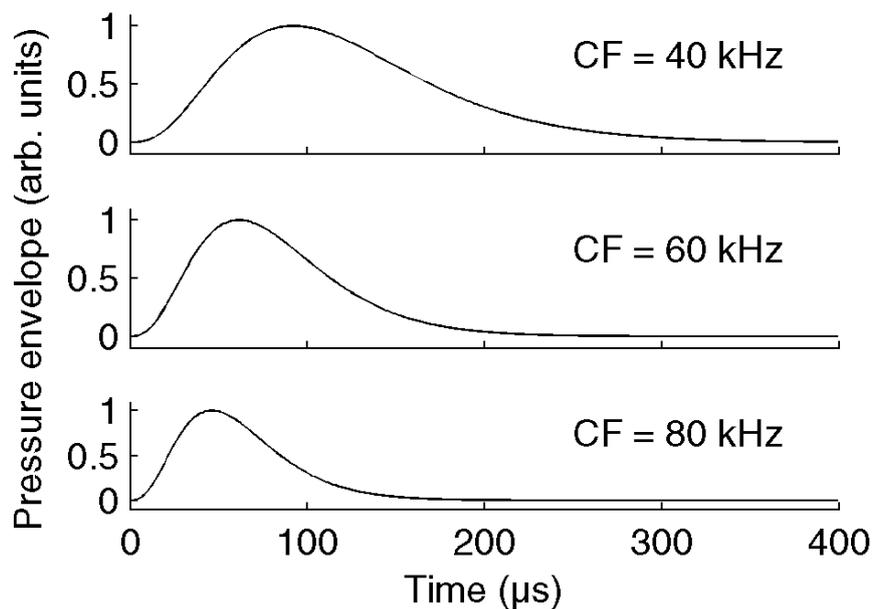
Figure 3.5: Three examples of an estimated temporal integration window for three different centre frequencies. The integration windows were generated by fitting a gammatone-filter transfer function to published suppression tuning curves (see text). Note how the duration of the integration window shortens with increasing centre frequency.

of a gammatone filter to the suppression tuning curves. The shape of the estimated integration window is illustrated in figure 3.5. With increasing frequency the auditory filters become broader, and consequently the integration window shortens. Even at a frequency of 80 kHz, the integration window spans almost 100 μs. Temporal integration in this order of magnitude has been shown for the bat *Megaderma lyra* and *E. fuscus* in a passive-acoustic paradigm (Surlykke & Bojesen, 1996; Weissenbacher et al., 2002; Wiegrebe & Schmidt, 1996). Note that this integration window and the temporal integration associated with the formation of the receptor potential in the inner hair cell are mandatory stages of auditory processing. Thus, the 305 μs threshold determined in the current experiment is in the range of peripheral auditory integration exhibited by the *P. discolor* cochlea.

3.5.3 Possible explanation for the deviant phase-jitter experiment results

Menne et al. (1989) performed an experiment where the authors implemented a pure phase jitter. Using a 27-coefficient finite impulse response (FIR) filter, they showed that *E. fuscus* could discriminate between two IRs that jittered in phase by 90 degrees. An

additional time jitter was used to preclude the bats' use of overall echo delay as a perceptual cue. The bats were able to detect the phase jitter superimposed on a random time jitter. At first sight, it appears difficult to reconcile these findings with our results. Therefore, we reconstructed the IRs described in and used by Menne et al. (1989). The analyses of echoes generated with the two phase-shifted IRs and a recorded *P. discolor* echolocation call are shown in figure 3.6. While there are very small and unsystematic differences in the Hilbert envelopes of the echoes (Figure 3.6, first row), the magnitude spectra of the echoes are identical (figure 3.6, second row).

These data confirm the authors' descriptions of the IRs. In the last row however, we show auditory spectrograms of the echoes as they are generated with a functional model of the *P. discolor* auditory periphery, described in detail in Grunwald et al. (2004). The degree of neural excitation is grey-scale encoded as a function of tonotopic frequency and time. The spectrograms reveal a significant difference between the auditory representations of the echoes generated with the phase-shifted IRs. The difference in the auditory spectrograms around 80 kHz most likely occurs due to the highly non-linear properties of the inner-hair cell half-wave rectification. This analysis indicates that the bats may have used spectral cues for the supposed phase discrimination. These cues occur despite the identity of the physical IR magnitude spectra. Similar cues were also found when the *P. discolor* call was replaced by a synthesized *E. fuscus* call. The current analyses stress the need for a physiologically plausible model of echo-acoustic processing over the purely physical description of the presented IRs. Human psychophysical studies have previously revealed the inadequacy of the Fourier transform to describe human perception (Patterson, 1994a; Wiegrebe et al., 1998).
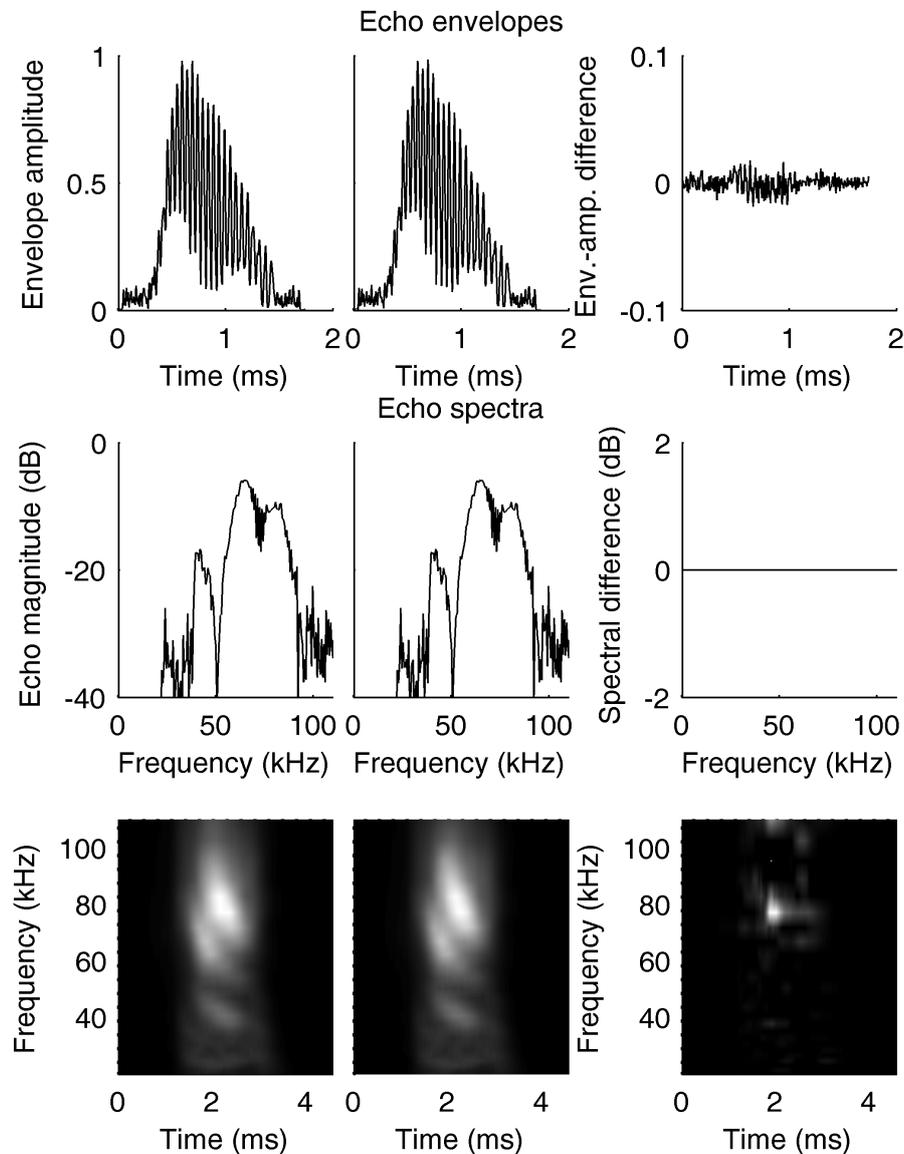
Figure 3.6: Physical and functional auditory analysis of the phase-shift experiment by Menne et al. (1989). Impulse responses with phase shifts of ±45° were generated as described in that paper. The first and second row show the echo envelopes and magnitude spectra generated with these IRs and an identical *P. discolor* call. The right-most column shows that differences in the envelope are very small and that the magnitude spectra are identical. The bottom row shows auditory spectrograms generated with the same echoes and a functional model of the *P. discolor* auditory periphery. Despite the identity of the magnitude spectra, the auditory model produces significant differences in the peripheral auditory representations of echoes generated with the two phase-shifted IRs.

3.5.4 Conclusion

To conclude: due to the different paradigm we used in our study, we cannot disprove a 10 ns performance threshold in delay-jitter experiments. However, we state that if this 10 ns threshold is correct, it does not demonstrate access of the bat to the complete echo phase spectrum, but only to that aspect of the phase spectrum that encodes echo delay. The current experiments show that a bat's access to the aspect of the phase spectrum which encodes IR duration is considerably less accurate and in qualitative agreement with temporal limitations of peripheral auditory processing. The current findings strongly suggest that the temporal resolution of echo-acoustic processing cannot be described with a single time constant, instead indicating that echo duration is encoded with a considerably lower temporal resolution than echo onset.

3.6 Acknowledgements

Concluding remarks

The projects composing this thesis investigated different aspects of the time domain analysis in echo-acoustic object analysis. One of these aspects is the roughness of an echo, which is basically dependent on the echo's amplitude changes over the echo's duration. Regarding the sensitivity of the bat *Phyllostomus discolor* for this echo roughness, we could demonstrate that there is a minimum echo roughness necessary for successful echo-roughness-based object discrimination. We also found that a minimum difference of 0.3 (log10M4) between two IRs is necessary to allow echo-roughness-based discrimination. Modifications of the stimuli-IRs used for these experiments, intended to produce more natural stimuli, had no significant impact on the discrimination performance of the bats. A qualitative comparison with echo-roughness data from natural objects, surveyed by Stilz (2004), gives reason to believe that the echo-roughness discrimination performance of *P. discolor* is sufficient for the classification of real trees or bushes.

However, this ability also entails problems. Imagine possible prey, like a small insect or the like, being positioned just in front of a tree's foliage. If an approaching bat ensonifies this insect, it also ensonifies the tree being just behind it. As the insect presumably just causes a single reflection, it could very well be that this reflection is in the bat's perception part of the tree's echo and therefore the insect remains undetected. It becomes backward-masked by the tree's echo. Of course, this depends on several factors: for one thing, the size of the insect and thus the resulting echo amplitude. If the insect's echo is loud enough compared to the subsequent tree's echo, the insect's echo should be distinguishable. For another thing, the distance between insect and tree, and therefore the time delay between the two echoes, will also effect the development of the backward-masking. Third, the type of tree, respectively the resulting echo roughness, should have an effect too. With a smooth echo, consisting of many small, closely succeeding reflections, the emerging of the backward-masking effect should be less likely then with a rough echo. In this case, due to the fewer reflections that also have longer delays be-

tween them, it is feasible that an additional reflection occurring prior to the actual tree's echo could be perceived as part of the tree's echo. Experiments concerning this topic are being conducted in our labs at the moment.

A different topic, albeit also relating to an echo's time domain, was addressed in chapter 3. Many studies pertained the question of how and to what degree a bat extracts information about the ensonified objects from the echo, for example Beedholm (2006); Firzlaff et al. (2007); Grunwald et al. (2004); Habersetzer & Vogler (1983); Hübner & Wiegrebe (2003); Schmidt (1988, 1992); Simmons (1971, 1973); Simmons et al. (1975). Some reach the conclusion that the highly precise performance that is exhibited by bats in echolocating tasks can only be explained by a detailed comparison of emitted call and echo, accomplished by the neural equivalent of a cross-correlation of call and received echo (Simmons, 1979; Simmons et al., 1990a). The spectrogram correlation and transformation model, for example, is based on this assumption (Saillant et al., 1993). The authors suggest for their model a reconstruction of the IR's time domain based on a recoding of the echo's spectral information into temporal information. A later study by Peremans & Hallam (1998) however demonstrated the limits of this model: the echo of the ensonified object may not possess more than two reflections, with at least 20 μs delay between them. In addition, the authors always used a copy of a bat's echolocation call to test the model, thus assuming that the ensonified object consists of only one plain reflecting surface. This is not the case for most natural objects, which usually comprise several different reflecting surfaces.

A different model by Matsuo et al. (2004) rejects the idea of a model based on a cross-correlation, as in the authors' opinion, cross-correlation alone is not sufficient to explain a bat's performance in classifying objects and delay times in 3D space (Matsuo & Yano, 2004). However, also the model proposed by Matsuo & Yano is based on time-domain reconstruction, as well applying a solely mathematical approach on the used stimuli.

The fundamental problem is, however, that both echolocation call and echo as they are available for the bat's auditory system, are the outcome of distinct, nonlinear conversions of the original call and echo that take place in the auditory periphery of the bat. As we demonstrated in chapter 3 in section 3.5.3, p. 57, this conversion can cause significant effects on the original echo, which are omitted in the mentioned models and thus might lead to erroneous results. In our lab, we are currently developing a new model of bat sonar (Wiegrebe, "An autocorrelation model of bat sonar", in prep.), which is based on a simulation of the auditory periphery of *P. discolor* and is already able to reproduce

the actual bats' performances in the experiments described in this thesis as well as the experiments described in (Schmidt, 1992; Weissenbacher & Wiegrebe, 2003).

Possible future projects

For both topics addressed in this thesis, open questions still remain. Concerning the discrimination of natural objects through roughness evaluation, there is by now a strong need for real IRs, recorded from bushes and trees in the natural habitat of *P. discolor*. Only thus would it be possible to know exactly if the roughness discrimination performance of *P. discolor* is really sufficient for the discrimination of natural objects in their natural habitat, or if it constitutes only an auxiliary discrimination option, with the actual discrimination process achieved in another, yet unknown way.

Regarding the phase sensitivity of bat sonar, there also are questions that still aren't answered. Although we could show that a general phase sensitivity, valid for all aspects of echo pase, is apparently not existent, this still leaves the 10 ns delay discrimination threshold reported by Simmons et al. (1990a) untouched. As the jitter-paradigm used to determine this threshold could be prone to flaws in the experimental design (Beedholm, 2006; Beedholm & Mohl, 1998), a different experimental setup is necessary to avoid these possible flaws. Currently, a project is implemented in our lab to determine the delay-sensitivity of the bat *Glossophaga soricina* using real targets instead of electronic delay lines. Of course, this requires strict verification that no other usable cue presents itself to the bat. Concerning the further examination of the extent of a bat's direct access to an echo's phase spectrum, one could try a repetition of the experiment done by Menne et al. (1989), already described in chapter 3, p. 57. Using the autocorrelation model currently developed in our lab, it should be possible to design a phase-modification process that keeps the duration of the utilized IR intact and doesn't exhibit spectral cues after being processed in the auditory periphery of the bat. The IR's duration should be significantly longer than the temporal integration time of the bat's auditory system to ensure better access to the available phase information. Quantification of this modification could for instance be achieved by partitioning of the phase spectrum in blocks of a defined size followed by a rearrangement. This way, neither delay nor duration of the IR can be used for discrimination. Possible factors worth investigating could for example be the block-size or the type of rearrangement - inversion of the block sequence, positioning of the last one, two or three blocks at the beginning

or vice versa. If the bat should still be able to distinguish IRs generated thus, an additional access to an echo's phase spectrum besides delay or duration has to be existing and could thus perhaps bring the connected question about the ability of bats to extract IRs out of echoes forward another step.

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List of abbreviations

AAF   anterior auditory field

AI   primary auditory cortex

IR   impulse response

CF   center frequency

DAP   data acquisition processor

FIR   finite impulse response

IC   inferior colliculus

$\log 10 M4$ base-10 logarithm of the fourth moment

M4   fourth moment

MMF   anaesthetic, consisting of Medetomidin, Midazolam and Fentanyl

PSTH   peri-stimulus time histogram

ROC   receiver operating characteristics

SAM   sinusoidally amplitude-modulated

xIR   cross-correlated impulse response, here created by cross-correlation of ensonification signal and echo

List of abbreviations

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