Spatial and temporal resolution of bat sonar

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Zusammenfassung

Während Menschen sich vor allem visuell orientieren und dabei auf externe Lichtenergie angewiesen sind, nutzen Fledermäuse ihre Fähigkeit zur Echoortung. Dabei senden Fledermäuse selbst Energie in Form von kurzen Ultraschallrufen aus. Diese Rufe werden von umliegenden Objekten reflektiert und die entstehenden Echos werden von Fledermäusen über ihre Außenohren aufgenommen. Durch den Vergleich von ausgesandtem Ruf und zurückkehrendem Echo können Fledermäuse Informationen über ihre Umgebung erlangen. Oft sind Fledermäuse von vielen Objekten umgeben, so dass ein Echoortungsruf zu zahlreichen Echos aus verschiedenen Richtungen führt, die je nach Entfernung der Objekte zu leicht unterschiedlichen Zeitpunkten bei der Fledermaus ankommen. In dieser Arbeit wird untersucht, mit welcher räumlichen und zeitlichen Auflösung Fledermäuse solch eine komplexe, natürliche Umgebung mit Hilfe der Echoortung analysieren können.

Im ersten Teil dieser Arbeit quantifizieren wir, wie gut Fledermäuse der Art *Phyllostomus discolor* ihre Wahrnehmung auf ein Zielobjekt fokussieren können und wie stark umliegende Objekte die Detektion des Zielobjekts beeinträchtigen. In einem sechs-kanaligen Phantomzielsetup mussten die Fledermäuse ein Zielobjekt, das entweder rechts oder links von der Fledermaus präsentiert wurde, detektieren. Zusätzlich wurden auf jeder Seite zwei maskierende Objekte präsentiert, die jeweils symmetrisch um die Zielposition angeordnet waren. Im Teilversuch zur aktiven Echoortung stellten die Zielobjekte und die maskierenden Objekte einfache Reflektoren dar, so dass die Rufe der Fledermäuse in Echtzeit unverändert zurückgespielt wurden. Im Teilversuch zur passiven Detektion hingegen, wurden den Fledermäusen künstliche Echoortungsrufe präsentiert. Die maskierenden Objekte wurden mit einer räumlichen Separierung zwischen 8° und 40° relativ zu den Zielobjekten angeordnet. Zusätzlich wurden Messungen durchgeführt, bei denen die maskierenden Echos mit einem zeitlichen Unterschied von bis zu 6 ms relativ zu den Zielechos präsentiert wurden. Die Ergebnisse dieses Experiments können dazu beitragen, ein verhaltenbasiertes räumlich-zeitliches rezeptives Feld des Echoortungssystems in *P. discolor* zu bemessen. Die Messungen zeigen, dass selbst bei einer räumlichen Separierung von 40° zwischen Zielobjekt und maskierendem Objekt keine vollständige Demaskierung stattfindet. Ferner deuten die Ergebnisse darauf hin, dass der Beitrag des empfangenden Teilsystems zur räumlichen Demaskierung deutlich höher ist als der des aussendenden Teilsystems. In den Versuchen zur zeitlichen Separierung von Zielobjekt und maskierendem Objekt war eine deutliche

Asymmetrie der Maskierung erkennbar: Nachverdeckung hatte einen wesentlich stärkeren Effekt als Vorverdeckung. Die Asymmetrie zwischen Nachverdeckung und Vorverdeckung war bei der aktiven Echoortung schwächer ausgeprägt als beim passiven Hören. Unsere Ergebnisse deuten ferner darauf hin, dass die aktive Echoortung, im Vergleich zum passiven Hören, zu einer zeitlichen Fokussierung des rezeptiven Feldes bei *P. discolor* führt. Die Ergebnisse werden zusätzlich durch die Quantifizierung der Breite der Emissionskeule sowie durch eine Simulation des Experiments ergänzt.

Der zweite Teil dieser Arbeit untersucht einen weiteren Aspekt der zeitlichen Auflösung der Echoortung bei Fledermäusen. Wenn Fledermäuse im Suchflug im offenen Raum fliegen, haben sie meist eine sehr geringe zeitliche Auflösung, da sie nur etwa alle 200 bis 500 ms einen Echoortungsruf aussenden. Zwischen zwei Rufen erhalten sie keine neuen Informationen über ihre Umgebung. Kurz bevor Fledermäuse ein Insekt fangen, senden sie allerdings einen so genannten „terminal buzz“ aus, in dem die Rufintervalle auf unter 6 ms sinken. Wir haben in Freifeld- und Laborexperimenten in der Fledermaus *Myotis daubentonii* untersucht, inwieweit Fledermäuse durch die hohen Emissionsraten im „terminal buzz“ den Nachteilen in der zeitlichen Auflösung, die durch die stroboskopische Art der Echoortung entstehen, entgegenwirken können. Dazu haben wir den Fledermäusen Beute in der Luft oder auf der Wasseroberfläche präsentiert und diese an verschiedenen Zeitpunkten vor dem Fang entfernt. Die Ergebnisse zeigen, dass das Echoortungsverhalten und die Fangbewegungen nicht stereotyp sind, sondern an Veränderungen während des „terminal buzz“ angepasst werden können. Die Reaktionszeit beträgt dabei etwa 100 ms, was im Vergleich mit anderen komplexen Verhaltensabläufen relativ kurz ist. Dies zeigt, dass die zeitliche Auflösung während des „terminal buzz“ hoch genug ist, um sehr schnelle Reaktionen zu ermöglichen und dass Fledermäuse wahrscheinlich dazu in der Lage sind, Nachteile die durch die diskontinuierliche Beschallung entstehen auszugleichen, indem sie Rufe mit hohen Wiederholraten aussenden.

Summary

While humans mainly use their visual sense, which is dependent on external light energy, for orientation, bats heavily rely on echolocation. When echolocating, bats themselves emit energy in form of short ultrasonic calls. These calls are reflected by surrounding objects and the resulting echoes are received via the bats' ears. By comparing the emitted echolocation call with the returning echo, bats are able to gain information about their environment. As bats are often surrounded by many objects, one echolocation call leads to numerous echoes from different directions which arrive at slightly different times at the bat, depending on the distance between each object and the bat. This thesis investigates the spatial and temporal resolution of bat sonar with which bats are able to analyze such a complex natural environment.

The first part of this thesis quantifies how well the bat *Phyllostomus discolor* can focus its perception on a target and how strongly surrounding objects impair the detection of the target. In a six-channel phantom object setup the bats had to detect a target that was presented either to the right or to the left of the bat. Additionally, two masking objects, which were arranged symmetrically around the respective target, were presented at each side. In the experiment about active echolocation, the target and the masking objects are simple reflectors, i.e. the bats' echolocation calls are played back to the bats in real time without modification. In the experiment analyzing passive detection performance, on the other hand, artificial echolocation calls are presented to the bats. The masking objects were positioned with a spatial separation between 8° and 40° relative to the targets. In addition, we conducted measurements in which the masking echoes were presented with a temporal difference of up to 6 ms relative to the target echo. The results of these experiments can be used to assess the behavioral spatio-temporal receptive field of *P. discolor*'s echolocation system. The measurements show that there is no complete release from masking, even at spatial separation of 40° between target and masking object. Furthermore, the results indicate that the contribution of the receiving subsystem to spatial unmasking is much higher than that of the emitting subsystem. The experiments about temporal separation of target and masker echoes show a clear asymmetry of masking: forward masking was much stronger than backward masking. The asymmetry of backward and forward masking was less pronounced in active echolocation than in passive hearing. Furthermore, our results indicate that the use of active echolocation leads to a

temporal sharpening of the spatio-temporal receptive field of *P. discolor*. Additionally, we quantified the width of the sonar beam and implemented a simulation of the experiment.

In the second part of this thesis, we investigated another aspect of the temporal resolution of echolocation in bats. During search flight in open space, bats usually have a very low temporal resolution because they emit an echolocation call only about every 200 to 500 ms. They are not able to gain information about their environment in between two adjacent echolocation calls. Shortly before catching an insect, bats emit a so called "terminal buzz" with call intervals down to less than 6 ms. In field and laboratory experiments we investigated if the bat *Myotis daubentonii* is able to compensate for the disadvantage in temporal resolution, which arises due to the stroboscopic nature of echolocation, by increasing the emission rate during the terminal buzz. We presented a prey object to the bats either in the air or on the water surface and removed the prey at different times before capture. The results show that the bats' echolocation behavior and capture movements are not stereotyped but can be adapted to changes even during the terminal buzz. The bats' reaction times were in the order of 100 ms. This is relatively short compared to other complex motor behaviors. This shows that the temporal resolution during the terminal buzz is high enough to allow for very fast reaction times and that bats are probably able to compensate for the disadvantages of a discontinuous ensonification by emitting calls at very high emission rates.

1 General introduction

How we perceive the world around us strongly depends on the sensory systems used to gather information about our surroundings. Most sensory systems are passive senses that depend on external energy to receive sensory input. In humans, for example, vision is reliant on external light, hearing on external sounds and smell on chemical molecules produced by other organisms. In some animals, active senses, in which the animals themselves produce the energy to sample the environment, have evolved. For example, deep-sea dragon fish use bioluminescence for vision (Denton *et al*. 1970; Oday & Fernandez 1974; Somiya 1982; Denton *et al*. 1985; Partridge & Douglas 1995) and weakly electric fish produce an electric field with which they can navigate and detect prey (for reviews, see Carr 1990; Assad *et al*. 1999; Bullock *et al*. 2005)

Another well studied active sense is echolocation. Echolocating animals actively emit echolocation signals that are reflected from surrounding objects. The returning echoes, that contain information about the objects from which they were reflected, are then analyzed by the animal (Neuweiler 2000). Sophisticated echolocation is known in bats and toothed whales. Toothed whales produce echolocation clicks with the monkey lips and dorsal bursae complex in the nasal apparatus. The signals are sent out via the melon (a fatty tissue at the forehead) and the echoes are received via the lower jaw and soft tissues around the lower jaw (Cranford & Amundin 2002; Vater & Kössl 2002). Bats, on the other hand, produce ultrasonic echolocation calls in their larynx, emit them through their mouth or nose and receive echoes via their outer ears (Neuweiler 2000). Bats are able to extract very detailed information about the environment from the echoes. The delay between the emitted echolocation call and the returning echo provides information about object distance (Simmons 1973) and binaural cues (differences in sound intensity and arrival time between the two ears) provide information about the horizontal position of objects (Erulkar 1972; Neuweiler 2000; Heffner *et al*. 2010). Monaural cues (angle-dependent filtering of sounds at the bat's outer ears, including the tragus), that also play a role in localization in the horizontal plane, are crucial for the bat to determine the elevation of objects (Wotton *et al*. 1996). Apart from this three-dimensional positioning of objects, bats are also able to discriminate different sized objects (Simmons & Vernon 1971; Simon *et al*. 2006) and objects differing in their surface structure (Habersetzer & Vogler 1983; Schmidt 1988; Schmidt 1992) or three-dimensional shape (Griffin *et al*. 1965; von Helversen & von Helversen 2003; Genzel *et al*. 2012).

In the acoustical domain each object is characterized by its acoustic image or impulse response (IR). An IR describes the resulting reflection characteristics of an object being ensonified with an impulse with a theoretical infinite short duration and infinite amplitude, containing every frequency with the same amplitude (fig. 1.1). Such an impulse is reflected differently by each reflective surface of the object. The object specific spectral interference patterns result from constructive and destructive interference of the different reflections and are visible in the magnitude spectrum of the IR as spectral peaks and notches.

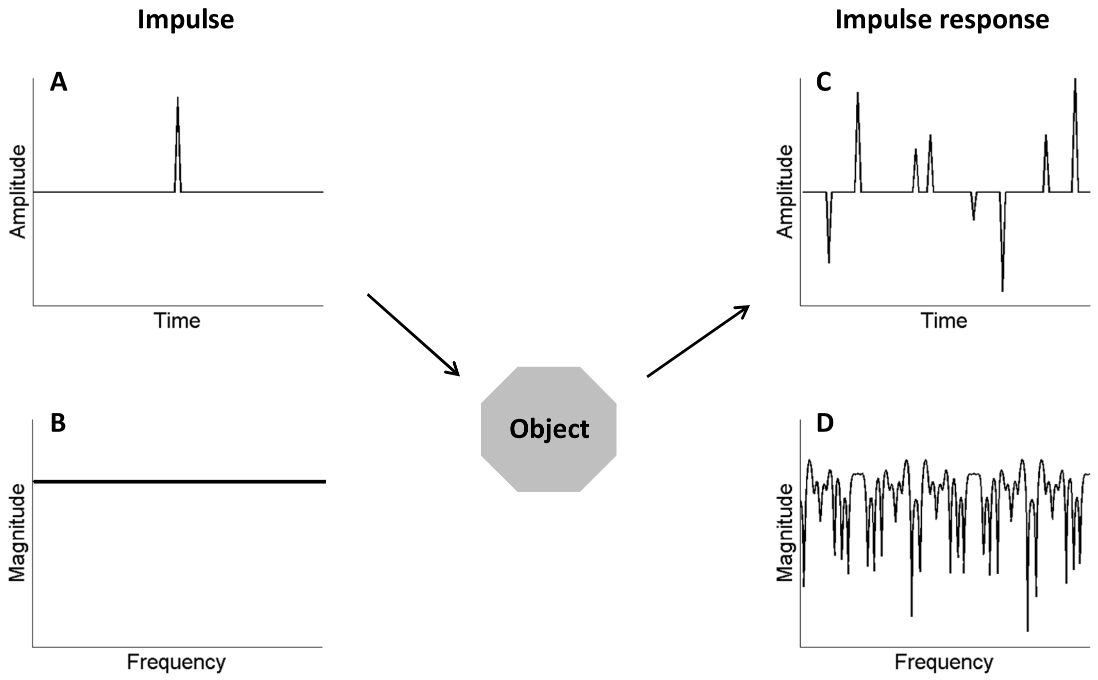

Figure 1.1: Impulse response (IR)
When an object is ensonified with an impulse (panel A), the impulse is reflected in an object-specific manner, leading to the IR of the object (panel C). While the impulse contains every frequency with the same amplitude (panel B), the magnitude spectrum of the IR shows characteristic spectral peaks and notches (panel D) resulting from constructive and destructive interference of the different reflections.
Panel A and B show the time signal, panel B and D the magnitude spectrum of the impulse or the IR, respectively.

When a bat ensonifies an object, however, it does not emit an impulse but an echolocation call. These calls are mostly brief and broadband in their spectral composition. However, they cannot be equalized with an impulse since they do not contain every frequency, are not infinitely short and do not have infinite amplitude. Thus, bats do not perceive the IR of an object directly, but an echo that contains information about the object and the emitted echolocation call. Mathematically, the echo results from the convolution of the IR with the echolocation call in the time domain (fig. 1.2). However, Weißenbacher (2003) could show that bats probably distinguish objects by analyzing the IR of the objects and not the echoes per se. This extraction of the IR is possible by a detailed comparison of the emitted call with the received echo. Mathematically, this can be achieved with the help of a cross correlation of the emission with the echo in the time domain, or, in the frequency domain, by multiplying the magnitude spectra of the echo and the emission and summing their phase spectra.

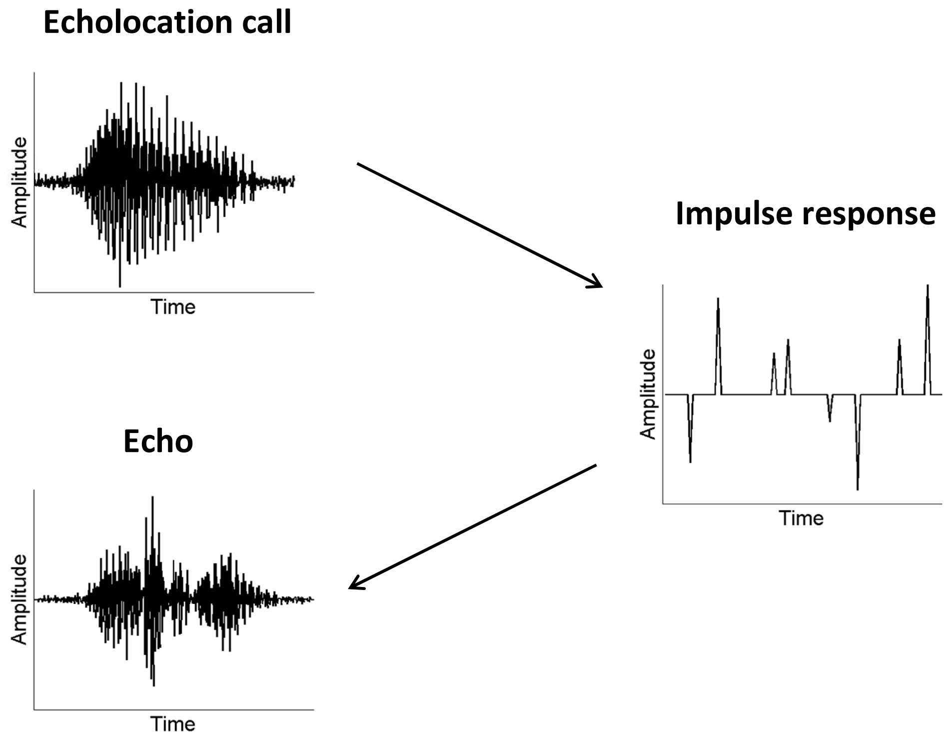

Figure 1.2: Echo generation
If a bat ensonifies an object, the returning echo results from the convolution of the emitted echolocation call with the IR of the ensonified object.
The graphs depict the time signal of the echolocation call, the IR of the object and the echo, respectively.

Thus, bats are able to gain information about objects by comparing their emitted echolocation call with the returning echo.

Many studies investigating echolocation have used virtual objects instead of real objects (e.g. Simmons 1973; Schmidt 1988; Aubauer & Au 1998; Weissenbacher & Wiegrebe 2003). A virtual object (VO) can be created by convolving a previously recorded or computer generated IR with a call emitted by an echolocating bat. The resulting echo is played back to the bat in real time. Thus, the bat perceives the object characterized by the IR although no real object is present. Virtual objects have the advantage that the object's reflection characteristics can easily be controlled and manipulated. Furthermore, virtual objects preclude that the bats use visual, olfactory or tactile cues to solve a task.

As echolocation is an active sense, bats can control the properties of their echolocation calls. Some specialized insect-eating bats, like e.g. *Rhinolophus hipposideros*, emit calls that have very long constant frequency elements. These calls are very narrowband signals and have a long duration (about 10-100 ms, fig. 1.3 A). Bat species emitting these kinds of calls often hunt insects in close proximity to vegetation. Their hearing system is specialized for the respective constant frequency component and they can even compensate for the Doppler-shift introduced by the forward motion of the bat. This call structure facilitates the recognition of flying insects because echoes reflected from beating wings, in contrast to echoes from the surrounding vegetation, are modulated in the rhythm of the wing beat (for reviews, see Schnitzler & Kalko 2001; Schnitzler *et al*. 2003).

Most known bat species, however, emit frequency modulated (FM) calls (fig. 1.3 B). Bats that mainly hunt in open space usually emit FM signals that are rather long and narrowband while bats mainly hunting in proximity to vegetation emit shorter and more broadband FM calls (for reviews, see Schnitzler & Kalko 2001; Moss & Surlykke 2010).

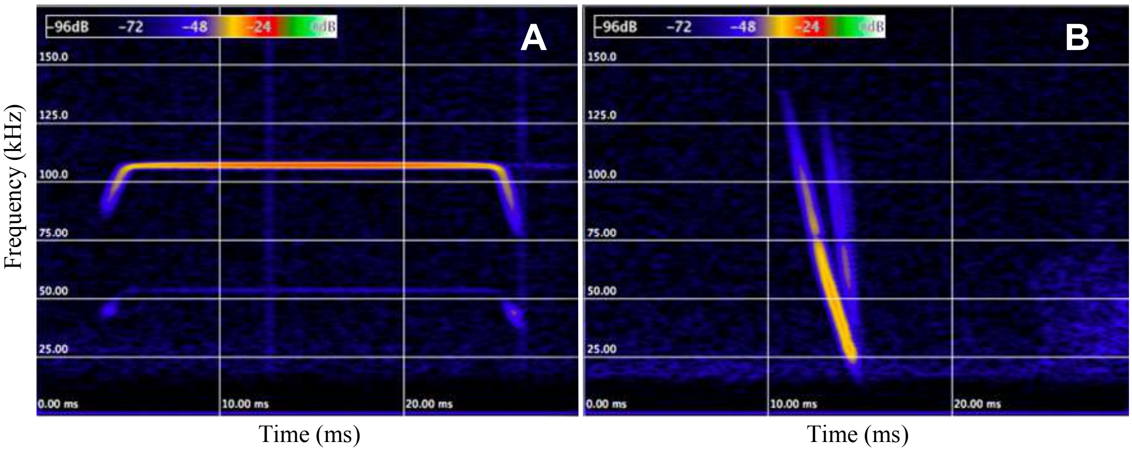

Figure 1.3: Exemplary echolocation calls
Spectrograms of an echolocation call with a long constant frequency element from *Rhinolophus hipposideros* (A) and of a frequency modulated echolocation call from *Myotis nattereri* (B). (Echolocation calls recorded by Michaela Gerges)

Apart from species-specific adaptations, bats can also adapt their echolocation signals to a given task. Generally, bats can exert control over the timing, the duration, the directionality, the frequency content and the intensity of their sonar emissions. For example, when a bat flies from an open area to a more cluttered area, it emits shorter calls with lower intensity and a broader bandwidth (reviewed in Moss & Surlykke 2010). It has also been shown that bats flying in open space in the field emit calls with a much higher directionality than in the laboratory that constitutes a more cluttered environment (Surlykke *et al*. 2009). A complex adaptive echolocation behavior can be observed when bats catch insects in the air or from the water surface. The bats' behavior can be subdivided into a search, an approach and a terminal phase (Griffin *et al*. 1960; Simmons *et al*. 1979). Search signals are rather long and narrowband which makes them well suited for prey detection. After detecting prey, the approach phase starts, the bats increase their calling rate and the calls are usually shorter and more broadband than in the search phase. During the terminal phase, which is initiated shortly before prey capture, bats emit short and rather broadband calls at an extremely high repetition rate. The calls emitted during the terminal phase are well suited for target localization and the high repetition rate provides a fast update of information (for reviews, see Schnitzler & Kalko 2001; Moss & Surlykke 2010).

A disadvantage of active sensing is that the production and emission of energy can be energetically costly for the organism (Nelson & MacIver 2006). During search flight the emission of echolocation calls in bats is coupled to the bat's wing beat and to expiration (Suthers & Suthers 1972). This coupling helps the bat to save energy (Waters & Wong 2007) and leads to no (Speakman & Racey 1991) or only a rather small (Waters & Wong 2007) energetic cost of echolocation during search flight. As there is no coupling between wing beat and call emission during the terminal phase, the energetic cost of echolocation might be higher during the terminal phase than during the search phase. However, this is not yet known.

It is also important to keep in mind that echolocation is a discontinuous sensing system. Bats perceive a "snapshot" of their environment with each echolocation call, but they do not receive any information in between their emissions (Nelson & MacIver 2006). A higher call repetition rate might impose higher energy costs. Furthermore, bats adjust their call rate to ensure that the returning echoes (especially from distant objects) arrive at the bats' ears before they emit a new call to ensure an unambiguous assignment of call and echoes (Jones 1999; Holderied & von Helversen 2003; Nelson & MacIver 2006). Thus, there is a trade-off between these factors and a higher temporal resolution of bat sonar (Nelson & MacIver 2006).

To catch flying insects with the help of echolocation in complete darkness is a very demanding task. It requires a very fast update of information and very fast reactions to changes in the insect's flight path. Furthermore, the bat does not only receive echoes from the insect but also from the surrounding vegetation. In comparison with the echoes from the insect, these masking echoes arise from different spatial positions and they arrive either simultaneously or at a slightly different time at the bat's ears. This means that the spatial and temporal resolution of bat sonar is very important for the bat to accomplish such a complex behavioral task in a natural environment.

The spatial resolution of bat sonar describes the ability of the bat to detect a target in the presence of masking objects at the same distance but at slightly different spatial locations. This ability depends on the directionality of the sonar emission and on the auditory spatial selectivity for echolocation calls. It is important to note that auditory spatial resolution is not the same as auditory spatial acuity. Auditory spatial acuity describes the ability to localize a test stimulus relative to a reference stimulus that has been presented before the test stimulus. It has been shown that the spatial acuity in the auditory system is very high (e.g. Mills 1958; Grantham 1986; Perrott & Saberi 1990; Grantham *et al*. 2003). The ability to detect a stimulus in the presence of other stimuli that are presented simultaneously at different spatial positions is termed auditory spatial resolution. Some studies indicate that the auditory spatial resolution is very bad in humans (Boehnke & Phillips 1999; Binetti 2009). As bats usually analyze high frequency sounds, the wavelengths of these sounds are relatively short compared to the size of the bats' pinnae. Thus the auditory spatial resolution might be higher in bats than in humans. As echolocation is an active sense, the bats' sonar emission also influences the spatial resolution of bat sonar. Since bats can move their ears and adapt the aim as well as the width of their emission, the focus of bat sonar is crucial for the spatial resolution of bat sonar.

In the first part of this thesis the spatio-temporal focus of bat sonar is investigated. As the bats' emitting and receiving system are both directional bats might be able to focus their echolocation system on a target of interest and blend out surrounding objects that impair the detection of the target of interest. We quantified the ability of the bat *Pyllostomus discolor* to focus its echolocation system on a punctiform reflector in a series of psychophysical experiments. The bats had to detect a target in the presence of two symmetrically arranged maskers that were positioned with an angular separation between 8° and 40° relative to the target. In another set of experiments target and maskers were separated spatially as well as temporally. This allows us to asses a behavioral spatio-temporal receptive field of *P. discolor*'s echolocation system.

The second part of this thesis focuses on temporal resolution of bat sonar in the context of echo-acoustic analysis of time-variant layouts. We conducted field and laboratory experiments with the bat *Myotis daubentonii* that catches insect from the water surface as well as in the air. While *M. daubentonii* emits echolocation calls at a repetition rate of about 10 Hz when flying through open space, it increases its call emission rate to up to 200 Hz shortly before it catches an insect. As the temporal resolution of bats is principally limited because of the stroboscopic nature of echolocation, we investigated the capture behavior of *M. daubentonii* to quantify how well bats are able to compensate for this limited temporal resolution by dramatically increasing the emission rate shortly before prey capture.

2 Spatio-temporal focus of bat sonar

Cornelia Geberl, Kathrin Kugler, Daniela Tietz and Lutz Wiegrebe

Lutz Wiegrebe and I designed the experiments and the analysis. I wrote the experimental programs, collected the data of the active-acoustic experiments (except the condition with a masker position of 40° and a signal delay -6 ms), conducted the analysis and wrote the manuscript. Lutz Wiegrebe and I supervised the diploma thesis of Kathrin Kugler and the thesis (Zulassungsarbeit) of Daniela Tietz. For their theses, Kathrin Kugler and Daniela Tietz collected the data of the passive-acoustic experiments and of the condition with a masker position of 40° and a signal delay -6 ms in the active-acoustic experiment. The program for the illustration of the synthetically produced echolocation call was written by Kathrin Kugler. I implemented the simulation of the experiment by adapting the auditory model of bat sonar that was conceived by Lutz Wiegrebe (Wiegrebe 2008).

2.1 Abstract

Echolocating bats orient by analyzing echoes of their ultrasonic emissions. In a cluttered environment it is important for bats to focus on a target of interest and to reduce the effect of masking echoes. We measured the spatio-temporal focus of bat sonar in *Phyllostomus discolor* in a six-channel phantom target setup. The bats had to detect a target signal that was symmetrically surrounded by two masking signals. The target signal and the masking signals consisted of the bats' own echolocation calls in the active-acoustic condition or of synthetically produced echolocation calls in the passive-acoustic condition. Target and masking signals were presented at angular separations between 8° and 40° and at temporal separations between 0 and 6 ms with the target signal either preceding or following the masking signals. The results can be used to assess the behavioral spatio-temporal receptive field of *P. discolor*'s echolocation system. When increasing the angular separation between target and masker from 8° to 40° in the simultaneous masking condition, the strength of masking decreased by 7 dB in the active-acoustic condition and by 6 dB in the passive-acoustic condition. Thus, the results indicate that the contribution of the receiving subsystem to spatial unmasking is much higher than that of the emitting subsystem. The bats showed a clear asymmetry of masking in the non-simultaneous temporal masking conditions with backward masking having a weaker effect on target detection than forward masking. However, the asymmetry of backward and forward masking was less pronounced in active echolocation than in passive hearing. Additionally, our results indicate that the use of active echolocation leads to a temporal sharpening of the spatio-temporal receptive field of *P. discolor*. Furthermore, we analyzed the directionality as well as the spectral characteristics of the bats' sonar emissions and implemented a simulation of the experiment to compare the expected performance of *P. discolor* in this specific experimental paradigm with our results.

2.2 Introduction

Echolocating bats are able to navigate through a highly cluttered environment in complete darkness by emitting ultrasonic echolocation calls and analyzing the returning echoes which arise when the echolocation calls are reflected by surrounding objects. When a bat ensonifies a complex echo-acoustic scene, many echoes will impinge almost simultaneously from many different directions onto the bat's ears. To perform a complex task like catching an insect that is surrounded by vegetation it is very important for the bat to resolve single reflectors from this multitude of echoes. How much masking objects impair target detection in bats strongly depends on the spatio-temporal focus of bat sonar. The spatial sensitivity of the bats' sonar system is determined by the radiation pattern of the emission system and the spatial selectivity of the receiving system. The radiation pattern of the bats' emitting system depends on the dimensions of the source (the mouth or nose) and the frequency content of the sound (Strother & Mogus 1970; Surlykke *et al*. 2009; Vanderelst *et al*. 2010) as well as on the shape of accessory acoustic elements (Schnitzler & Grinnell 1977; Zhuang & Muller 2006). The directionality of the bats' receiving system mainly depends on the size and shape of the bats'outer ears (Grinnell & Schnitzler 1977; Guppy & Coles 1988; Obrist *et al*. 1993; Firzlaff & Schuller 2003). Additionally, many bats show outer-ear movements which are often synchronized with sonar emissions. These movements will also contribute, and add a dynamic component, to the spatial receptive field of the bats' echo-imaging system. Outer-ear movements have mainly been studied in horseshoe bats (Mogdans *et al*. 1988; Gao *et al*. 2011). The directionality of the bats' emission system has been measured in the laboratory (e.g. in *Myotis grisescens*: -6 dB points at 38° lateral at 75 kHz and at 30° lateral at 95 kHz (Shimozawa *et al*. 1974) or in *Rhinolophus ferrumequinum*: -6 dB points at 23° lateral (Schnitzler & Grinnell 1977)) and in the field (in *Myotis daubentonii*: -6 dB points at 25° lateral at 40 kHz and at 14° lateral at 75 kHz (Surlykke *et al*. 2009)).

The directionality of the receiving system can be addressed by measuring the head related transfer function (HRTF) which describes the spatial filtering of sounds that takes place at the head and the outer ears before the sound reaches the animal's tympanum (Young *et al*. 1996; Hartmann 1999; Firzlaff & Schuller 2004; Vanderelst *et al*. 2010). The acoustic cues that are generated by the bats' head and outer ears have been measured for different bat species (Guppy & Coles 1988; Obrist *et al*. 1993; Wotton *et al*. 1995; Fuzessery 1996; Firzlaff & Schuller 2003). For *Phyllostomus discolor* the directionality of the emitting system and of the receiving system as well as the resulting directionality of its whole echolocation system has been simulated (Vanderelst *et al*. 2010). The simulation indicates that, especially at high frequencies, the directionality of the whole echolocation system is higher than the directionality of the emitting or receiving system alone.

The spatial selectivity of the bats' sonar system strongly influences to which extent echoes from surrounding objects impair the perception of a target of interest. This situation in which a target echo is masked by echoes of other objects close to this target is called clutter interference (Simmons *et al*. 1988). Clutter interference is often encountered by bats, especially if they hunt insects close to background vegetation.

Generally, two different forms of masking can be distinguished: simultaneous masking, in which the masking sound is present throughout the presentation of the target sound, and non-simultaneous masking in which the target sound is temporally separated from the masking sound. Non-simultaneous masking can be subdivided into forward masking in which the target signal follows the masking signal and into backward masking in which the target signal precedes the masking signal (Moore 2008).

Many studies have investigated masking phenomena in bats (e.g. Simmons *et al*. 1988; Simmons *et al*. 1989; Møhl & Surlykke 1989; Arlettaz *et al*. 2001; Lu & Jen 2002; Faure *et al*. 2003; Luan *et al*. 2003; Luan *et al*. 2005; Stamper *et al*. 2008; Aytekin *et al*. 2010; Bates *et al*. 2011).

When the target signal and the masking signal are spatially separated, the strength of masking decreases compared to a situation where target and masker are at the same place. This so called spatial unmasking has for example been shown for humans (Saberi *et al*. 1991; Peissig & Kollmeier 1997; Kidd *et al*. 1998; reviewed in Bronkhorst 2000), birds (Dent *et al*. 1997; Dent *et al*. 2009) and frogs (Nityananda & Bee 2012). Sümer *et al.* (2009) investigated spatial unmasking in the bat, *Eptesicus fuscus*. The bats had to detect a wire that was positioned 11 cm in front of an angular masker. The masker was positioned at different azimuthal angles between masker and wire and the threshold diameter of the wire was measured for each masker position. For an angular separation of 23° between wire and masker, the authors measured a complete release from masking, i.e. the masker did no longer impair the detection of the wire.

Most of the studies that investigated spatial unmasking used only one masker. Studies in humans in which a target signal in front of the subjects was masked by two maskers that were symmetrically arranged around the target with different angular separations showed a much weaker spatial unmasking effect compared to studies with only one masker (Bronkhorst & Plomp 1992; Bronkhorst 2000). When the maskers consisted of uncorrelated noise no spatial unmasking was achieved up to angular separations between target and masker of 30° (Noble & Perrett 2002) or 90° (Binetti 2009). These results together with experiments that allow conclusions to be drawn about the size of the spatial receptive fields in humans (Boehnke & Phillips 1999; Salminen *et al*. 2009), cats (Mickey & Middlebrooks 2003) and rhesus monkeys (Werner-Reiss & Groh 2008) indicate two broad spatial receptive fields that cover the left and the right hemisphere, respectively.

Since bats, in contrast to humans, usually analyze the echoes of their ultrasonic echolocation calls, the wavelengths of the analyzed sounds are relatively short compared to the size of their pinnae. Furthermore, bats might be able to use the maneuverability of their ears to focus their attention on a target of interest. In an active-acoustic target detection task bats can probably also use the directionality of their emission to reduce masking effects of spatially separated objects. This might lead to a higher auditory spatial selectivity and more focused spatial receptive fields in bats than in humans. As masking in bats has not been systematically studied with maskers being arranged symmetrically around a target, the spatial receptive field of bats has not been quantified up to now.

This study aims to quantify the spatio-temporal focus of bat sonar and the auditory spatial selectivity in a series of formal psychophysical phantom-target experiments in the bat, *P. discolor*. In a two-alternative forced choice six-channel phantom-target paradigm the bats were trained to detect a target that was symmetrically surrounded by two maskers. That means they had to decide between one side from which a target signal and two masking signals were played back and one side from which only the two masking signals were played back. The maskers could be positioned with an angular separation between 8 and 40° relative to the target. The target signal as well as the masking signals consisted of the bats' own echolocation calls in the active-acoustic experiments and of synthetically produced echolocation calls in the passive-acoustic experiment. We measured the target detection thresholds without maskers, with different angular separations between target and masker and with different time intervals between target signal and masking signals in an active-acoustic and a passive-acoustic condition. This allowed us to assess a behavioral spatio-temporal receptive field of *P. discolor*'s echolocation system and of its receiving subsystem alone.

2.3 Methods

2.3.1 Experimental animals

Nine male and two female adult neotropical bats of the species *P. discolor* were used in the experiments. *P. discolor* is omnivorous and mainly feeds on nectar, pollen, flowers, fruit and insects (Kwiecinski 2006). The echolocation calls of *P. discolor* are downward-modulated, multi-harmonic and cover a frequency range between 45 and 100 kHz (Rother & Schmidt 1982; Kwiecinski 2006). Training took place at 5 consecutive days a week. At these days the bats were housed together in a cage (80 x 60 x 80 cm) before the training session. During the remaining time the bats were kept in a 12 m^2 flight room. The bats' nutrition consisted of fruit pulp which the bats received as a reward in the training sessions and a combination of mealworms and fruit during the two days without training. Except during the individual training sessions, the bats had free access to water.

2.3.2 Experimental setup

We implemented a virtual playback paradigm in which the bats had to evaluate echoes of their own echolocation calls which were played back to them in real-time. Experiments took place inside a foam-coated, echo-attenuated chamber. The bats were trained in a two-alternative, forced-choice setup. It consisted of an inversely mounted Y-maze with a starting position at the upper end and a feeder at the end of each leg. We implemented six virtual target units, each consisting of a microphone (Sanken CO100K, Tokyo, Japan) and an ultrasonic speaker (Matsushita EAS10TH800D, Technics Matsushita, Osaka, Japan). The six speakers were attached to a metal ring with a radius of 80 cm. The microphones were mounted 42 cm in front of the speakers. The surface of the speakers (except the speaker membrane) and the surface of the metal ring were covered with acoustic foam. The target signal was played back by either the second or the fifth virtual object unit (targets) being located in the left and the right hemisphere of the bat, respectively. Each of the targets was symmetrically surrounded by two virtual object units (maskers) which were used to play back masking signals. While the position of the targets was fixed, the maskers could be moved manually to achieve angular separations between 8° and 40° between a masker and its corresponding target. The setup is depicted in figure 2.1.

Stimulus presentation and data acquisition were controlled by a computer running MATLAB 7.5 (Mathworks, Natick, MA) with the professional MATLAB audio tool

SoundMexPro (HörTech gGmbH**,** Oldenburg, Germany). When a trial was started in the active acoustic experiments, emitted echolocation calls were recorded by the six microphones, amplified, high-pass filtered at 20 kHz (Octamic II, RME, Haimhausen, Germany) and digitalized by an audio interface (Fireface 800, RME, Haimhausen, Germany) at a sampling rate of 192 kHz. The calls were convolved with the compensatory impulse response of the microphones, high-pass filtered at 30 kHz and attenuated on each channel individually (see 'Experimental conditions' below). In experiment 2 and 3 an implemented trigger ensured that playback was only started when the bat emitted an echolocation call. The virtual echoes were digital to analogue converted by the audio interface, amplified (RB-976MKII, Rotel, Worthing, England) and played back to the bat via the speakers. The input-output delay was 3.8 ms for experiment 1 and 4.2 ms for experiment 2 and 3.

In the passive acoustic experiment the microphone preamplifiers were turned off and synthetically produced echolocation calls (see 'Experimental conditions' below) were digital-to-analogue converted by the audio interface, amplified (RB-976MKII, Rotel, Worthing, England) and played back to the bat via the speakers.

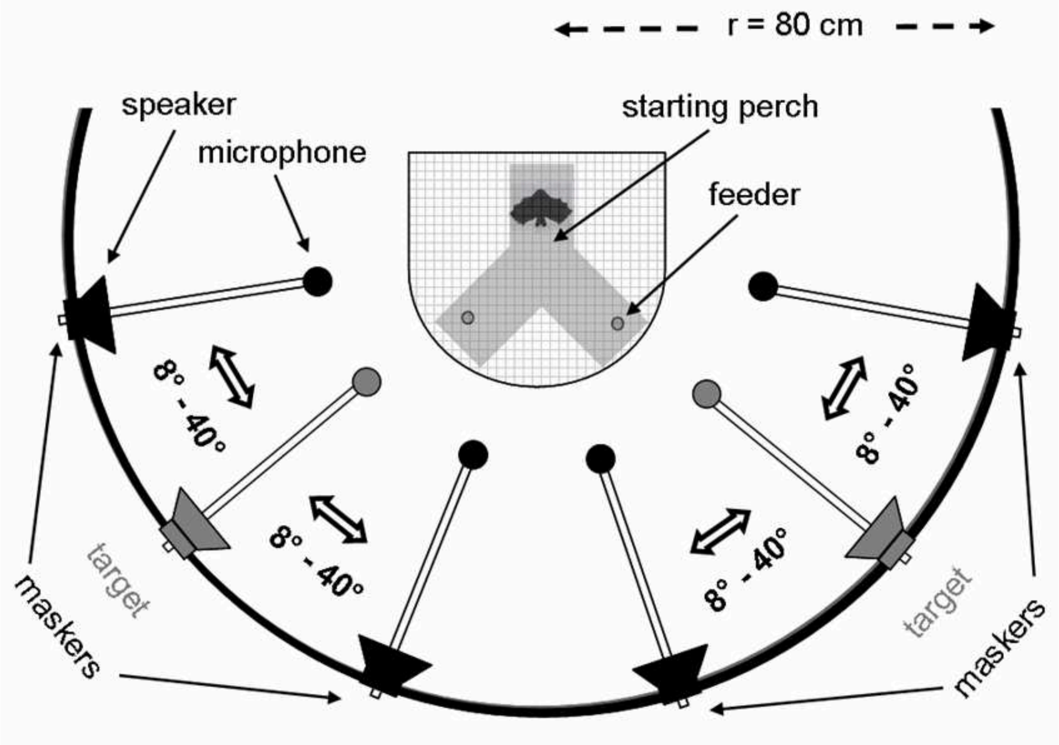

Figure 2.1: **Experimental setup**
The experimental setup is built up of a Y-maze and six virtual object units, each consisting of a microphone and a loudspeaker. The target signals were played back by the second or the fifth virtual object unit (targets, depicted in grey) and the masking signals by the remaining four virtual object units (maskers, depicted in black) which were positioned with an angular separation between 8° and 40° relative to the corresponding target.

2.3.3 Experimental conditions

All virtual objects were implemented as simple reflectors.

2.3.3.1 Experiment 1: Spatial focus of bat sonar

In experiment 1, in which the bats had to evaluate echoes of their own echolocation calls, the virtual objects were presented at a distance of 1.2 m. We recorded the ability of the bats to detect the target echo in absence of masker echoes by attenuating the masker echoes by 200 dB. The target strength of the target was varied between 0 dB and -42 dB in steps of 6 dB.

In the masking conditions the target signal was symmetrically masked by two masking signals. The angular separation between each masker and the target was either 40°, 28.3°, 20°, 12.4° or 8°. The target strength of the maskers was fixed to -12 dB in all conditions with maskers. The target strength of the target was varied between 0 dB and -36 dB in steps of 6 dB.

2.3.3.2 Experiment 2: Spatial focus of bat sonar: Control

To make sure that the bats did not use passive information to solve the task in experiment 1, we implemented a trigger in experiment 2. Thus, playback was only started when the bat actively emitted an echolocation call. Every time the bat’s echolocation call exceeded a predefined threshold level, playback was turned on for 2.45 ms (0.45 ms before, and 2 ms after the threshold was exceeded). Afterwards, no playback could be started for 18 ms. The virtual object distance was 3.0 m (corresponding to an absolute call-echo delay of 17.4 ms). In the condition without maskers in experiment 2 the target strength of the maskers was set to -200 dB and the target strength of the target was varied between -12 dB and -45 dB in steps of 3 dB. In the masking conditions, the angular separation between each masker and the target was either 40°, 20° or 8°. The target strength of the maskers was fixed to -12 dB in all conditions with maskers and the target strength of the target was varied between +12 dB and -33 dB in steps of 3 dB.

2.3.3.3 Experiment 3: Spatio-temporal focus of bat sonar

In experiment 3 we investigated how a temporal separation of target and masking signals effects spatial unmasking. In the condition without maskers, the target strength of the maskers was set to -200 dB and target strength of the target was varied between 0 dB and -48 dB in steps of 3 dB. To test whether the emitted echolocation call influences the detectability of the target echo, we played back the target echo with an absolute delay of 8.4, 11.4 and 23.4 ms (a delay of 17.4 ms was already presented in experiment 2).

In the masking conditions, the angular separation between each masker and the target was either 40° or 8°. The target strength of the maskers was fixed at -12 dB in all conditions with maskers and the target strength of the target was varied between +6 dB and -33 dB in steps of 3 dB. While the masking echoes were always played back with an absolute delay of 17.4 ms (virtual object distance of 3 m), the delay of the target echoes was set to 11.4, 14.4, 20.4 or 23.4 ms. This means that we created a backward masking situation in which the target echo preceded the masking echoes by 3 or 6 ms or a forward masking situation in which the target echo followed the masking echoes after 3 or 6 ms. When the data is expressed in terms of signal delay, time intervals between target signal and masking signals are given as negative values (-3 and -6 ms) for backward masking situations and as positive values (3 and 6 ms) for forward masking situations.

2.3.3.4 Experiment 4: Auditory spatio-temporal selectivity for echolocation calls

To investigate the spatial focus of the emitting system and the receiving system independently from one another, we conducted a passive acoustic experiment in which the bats did not need to echolocate but had to detect a passively presented target signal in the presence of masking signals. The target signal as well as the masking signals were synthetically produced echolocation calls. The calls were generated in MATLAB v. 7.5 and resembled a typical echolocation call of *P. discolor* with a duration of 1.5 ms and four harmonics with the first harmonic starting at 23 kHz, downward sweeping to 19 kHz. The first harmonic was attenuated by 30 dB, the second, third and fourth harmonic by 10 dB, 5 dB and 0 dB, respectively (figure 2.2). Since the signals were sampled at 192 kHz, the fifth harmonic was not presented as it contains frequencies above 96 kHz. The signals were presented with a repetition rate of 2 Hz. To prevent the bats from solving the task by comparing the overall sound level of the two sides, a roving level of ± 6 dB was applied to the two sides independently.

In the condition without maskers in experiment 4 the level of the masking signals was set to -112 dB peak-equivalent sound pressure levels (dB pe SPL) and the target echo was played back with a level between 70 dB pe SPL and 13 dB pe SPL in steps of 3 dB. In the masking conditions, the angular separation between each masker and the target was either 40°, 20° or 8°. The level of the masking signals was fixed to 49 dB pe SPL and the level of the target signal was varied between 73 dB pe SPL and 28 dB pe SPL in steps of 3 dB. The target signal was either presented at the same time as the masking signals, 6, 3, 1.5 ms before or 6, 3 ms after the masking signals. Thus, as in the active acoustic experiment we created a simultaneous, a backward and a forward masking situation. When the data is expressed in terms of signal delay, time intervals between target signal and making signals are given as negative values (-1.5, -3 and -6 ms) for backward masking situations and as positive values (3 and 6 ms) for forward masking situations.

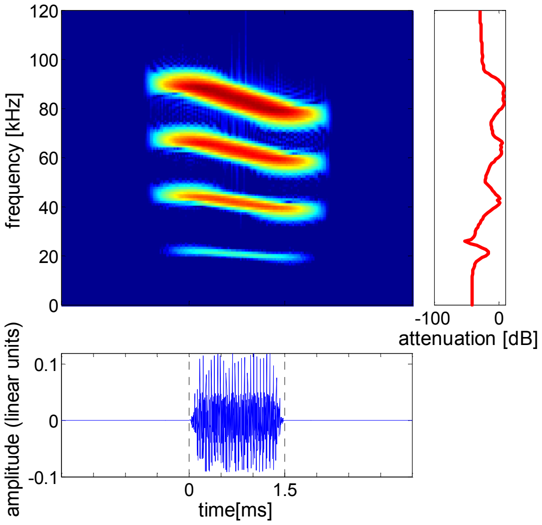

Figure 2.2: Synthetically produced echolocation call
Depicted are the spectrogram (top, left), the time course (bottom) and the amplitude spectrum (top, right) of the synthetically produced echolocation call.

2.3.4 Procedure

In conditions without maskers, only the target signal was played back either from the left or from the right side. In conditions with maskers, the bats had to decide between one side at which the target signal was symmetrically masked by two masking signals, and the second side from which only the two masking signals but no target signal was played back. In both cases the bats were trained to crawl towards the end of the leg of the Y-maze where the target signal was played back. Correct decisions were rewarded with fruit pulp. The site on which the target signal was presented was chosen pseudorandomly (Gellermann 1933). Data acquisition started when the bats showed a stable performance of ≥ 85 % correct choices over three consecutive training days. Psychometric functions, with 30 trials for each target signal attenuation, were obtained. A sigmoid function was fitted to the psychometric function and the discrimination threshold was set to 75 % correct choices (significance level: $p < 0.003$). To calculate the strength of masking, we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions for each bat. Afterwards, we averaged the strength of masking over all bats. In experiment 2 and 3 we measured the thresholds without masking for four different absolute call-echo delays (8.4, 11.4, 17.4 and 23.4 ms). In the conditions with masking signals in experiment 3, the target signals were played back with a call-echo delay of 11.4, 14.4, 20.4 or 23.4 ms. For the calculation of the strength of masking, we compared the threshold of the different masking conditions with the threshold that was obtained without masking signals at the corresponding call-echo delay. For the call-echo delays at which no threshold without maskers was measured (14.4, 20.4 ms and for bat 2 also 11.4 ms), we interpolated the thresholds obtained for neighboring call-echo delays.

2.3.5 Sound analysis

During data acquisition, the echolocation calls picked up on each of the six microphones during the last 4 s of each trial were saved. We analyzed the directionality and the spectral characteristics of the bats' echolocation calls in experiment 1. We did not include the last second of the recordings in our analysis as this was approximately the time that the bats needed to crawl from the starting perch to the end of the leg of the Y-maze. The recordings were analyzed automatically by a custom-written program (MATLAB 7.5). The automatic call detection as well as the spectral analysis is based on a routine written by Holger Goerlitz (Goerlitz *et al*. 2008).

2.3.5.1 Directionality analysis

To determine the directionality of the echolocation calls, we calculated the RMS level of each call on each channel for a certain masker position. We selected the calls that were directed towards a target, i.e. had their maximal amplitude at the second or the fifth microphone. The levels on the six channels were normalized for each call so that the highest level was set to 0 dB. The normalized RMS levels of each channel were averaged either over all calls of all six bats (fig. 2.13) or over all calls for each bat individually (fig. 2.14). We did this calculation for each masker position (40°, 28.3°, 20°, 12.4° and 8°) separately and combined the results to get the mean normalized RMS levels on 22 different spatial positions for the case that the left target was ensonified and the mean normalized RMS levels on 22 different spatial positions for the case that the right target was ensonified. Assuming that the bats' sonar emission is symmetrical, we combined these two data sets to obtain the mean normalized RMS levels for 33 different spatial positions (figure 2.3). We fitted a Gaussian to this data and characterized the directionality of the calls by determining the angle at which the Gaussian is 3 or 6 dB below its peak (-3 and -6 dB angle, respectively). Apart from analyzing the directionality of the broadband calls we also analyzed the directionality of the second and the fourth harmonic of the calls. Therefore, the bats' echolocation calls were band-pass filtered around a centre frequency of 38 or 76 kHz, respectively, with a bandwidth of ± 10 % of centre frequency and a slope of 24 dB/octave.

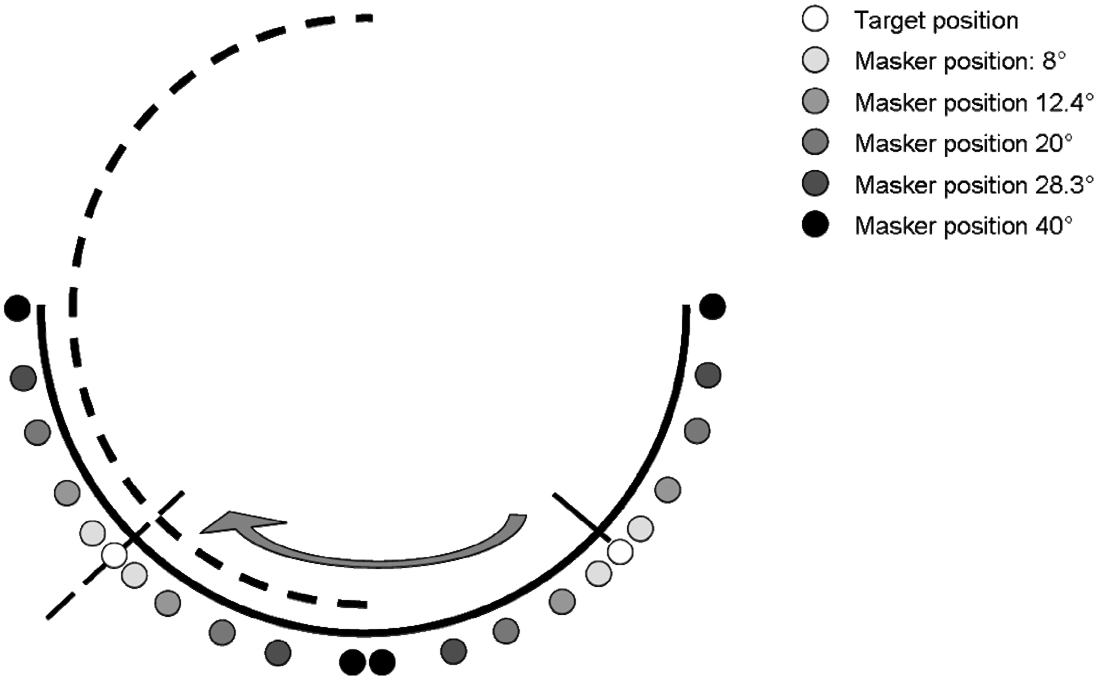

Figure 2.3: Determining the directionality of the echolocation calls
The figure illustrates how we combined our sound recordings to calculate the levels of the echolocation calls at 33 different spatial positions to determine the directionality of the echolocation calls. We selected all calls that were directed towards the left target and calculated the levels on the six microphones. As the microphones of the maskers were positioned at five different target-masker separations we obtained measurements at 22 different spatial positions (depicted as small circles). We assumed that the calls are symmetrical and combined this data set with the data set where the bat echolocated towards the right target (indicated by the two hemicycles). This leads to measurements at 33 different spatial positions.

2.3.5.2 Spectral analysis

For the spectral analysis we determined the best frequency, the frequency centroid and the fundamental frequency of each call. Median values were calculated for each bat. The fundamental frequency was determined from the frequency distribution of the fourth harmonic.

2.3.6 Simulation

To simulate the expected performance of *P. discolor* in our active acoustic experimental paradigm we used spatial sensitivity patterns of *P. discolor*'s emitting and receiving system that were simulated by Vanderelst *et al.* (2010) and designed an auditory model which closely follows the auditory model of bat sonar described by Wiegrebe (2008). We simulated the situation that the bat echolocates towards the left and the right target and compares the returning echoes from both sides with the signal that the bat had associated with a food reward during many above threshold training trials. To create the target echo we convolved the artificial echolocation call described in experiment 4 with the bat's frontal emission radiation pattern (0°) and its frontal HRTF. Masking echoes were created by convolving the artificial echolocation call with the emission radiation pattern and the HRTF at -40, -20 or -7.5° for the first masker and at 40, 20 or 7.5° for the second masker. We used 7.5° instead of 8° because the spatial sensitivity patterns were calculated in steps of 2.5°. The bat has to discriminate between a signal side that consists of the target echo and the two masking echoes and a standard side that only consists of two masking echoes. All masking echoes were attenuated by 12 dB and the attenuation of the target echo varied between 0 and 60 dB. The resulting in ear signals are processed by the bat's middle and inner ear. As in Wiegrebe (2008), the transfer characteristics of the middle ear are simulated by a broad band-pass filter, the frequency-to-place conversion at the basilar membrane in the inner ear is simulated by a gammatone filter bank and the non-linear transformations of the organ of corti are simulated by a half-wave rectification and an exponential compression. Temporal integration was implemented by a 1 kHz low-pass filter with a slope of 12 dB per octave. By adding random noise with a fixed variance the overall encoding accuracy of the model is reduced. In contrast to Wiegrebe (2008) no strobed, normalized autocorrelation is used. When the bat associates the signal side with a food reward during training, it forms a template of the rewarded signal. To create a template in our simulation, we averaged the output of the model across 20 presentations of the signal which consists of the target echo attenuated by 0 dB and the two masking signals attenuated by 12 dB. To generate the psychometric function, the Euclidean distances between the model output of the signal side and the template as well as between the model output of the standard side and the template are calculated. The difference between these two Euclidean distances was used as input to the decision device developed by Dau *et al.* (1997).

For the simulation of the expected performance of *P. discolor* in our passive acoustic experimental paradigm we used the same simulation as for the active acoustic paradigm, except that the artificial echolocation calls were only convolved with the corresponding HRTF, but not with the bat's emission radiation pattern.

2.4 Results

2.4.1 Psychophysics

2.4.1.1 Experiment 1: Spatial focus of bat sonar

In this active-acoustic experiment, in which the spatial focus of bat sonar is analyzed, psychometric functions were obtained from six bats for the condition without masker and for five different masker positions. The presented data is based on 6210 trials. Figure 2.4 shows the performance data and the fitted sigmoid functions for all conditions exemplarily for bat 1. Threshold levels for the different conditions are given in the legend. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. The strength of masking for each individual bat is given in table 2.1. Figure 2.5 illustrates the strength of masking averaged over all bats. When increasing the angular separation between target and masker from 8° to 40° the strength of masking decreased by 7 dB (from 11.5 to 4.5 dB).

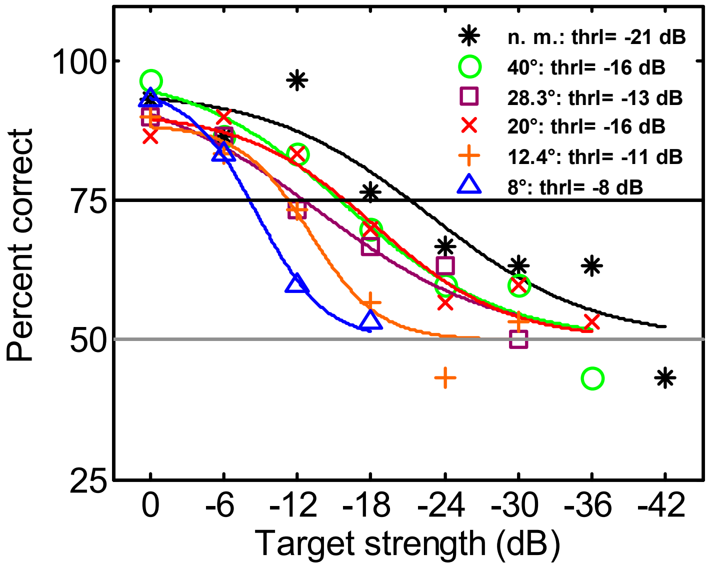

Figure 2.4: Psychometric functions for bat 1 in experiment 1
The symbols represent the percent correct choices of bat 1 in experiment 1 at different target strengths. The results for the condition without masker (black) and for the conditions with maskers at different target-masker separations are shown (40°=green, 28.3°=lilac, 20°=red, 12.4°=orange and 8°=blue). Performance decreased with decreasing target strength. For each condition a sigmoid function (solid lines) was fitted to the data and the perception threshold (thrl) was calculated as the intersection point of the sigmoid function with the 75 % correct value (black horizontal line).

	Strength of masking (dB)					
Condition	**Bat 1**	**Bat 2**	**Bat 3**	**Bat 4**	**Bat 5**	**Bat 6**
40°	6	9	5	-1	4	4
28.3°	9	13	8	1	5	9
20°	5	14	3	2	2	8
12.4°	10	18	9	3	9	10
8°	13	18	10	6	10	13

Table 2.1: Strength of masking in experiment 1
The table shows the strength of masking (dB) for each bat in experiment 1 for the five different target-masker separations (40°, 28.3°, 20°, 12.4° and 8°). To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions.

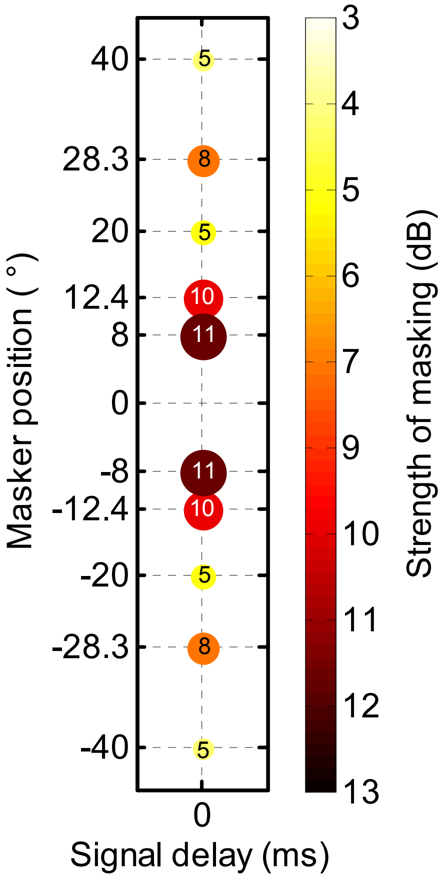

Figure 2.5: Mean strength of masking in experiment 1
The numbers as well as the color and size of the data points depict the strength of masking, averaged over all bats, in experiment 1 for the five different target-masker separations (40°, 28.3°, 20°, 12.4° and 8°). To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. To illustrate the symmetrical masking paradigm, the results have also been plotted at -8°, -12.4°, -20°, -28.3° and -40°.

2.4.1.2 Experiment 2: Spatial focus of bat sonar: Control

In the active-acoustic control experiment data was obtained from five bats for the condition without masker and for three different masker positions. The presented data is based on 5220 trials. Performance data and the fitted sigmoid functions of bat 3 are shown in figure 2.6. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. The strength of masking for each individual bat is given in table 2.2. Figure 2.7 illustrates the strength of masking averaged over all bats. Consistent with experiment 1, the strength of masking decreased by 7 dB when the angular separation between target and masker was increased from 8° to 40°.

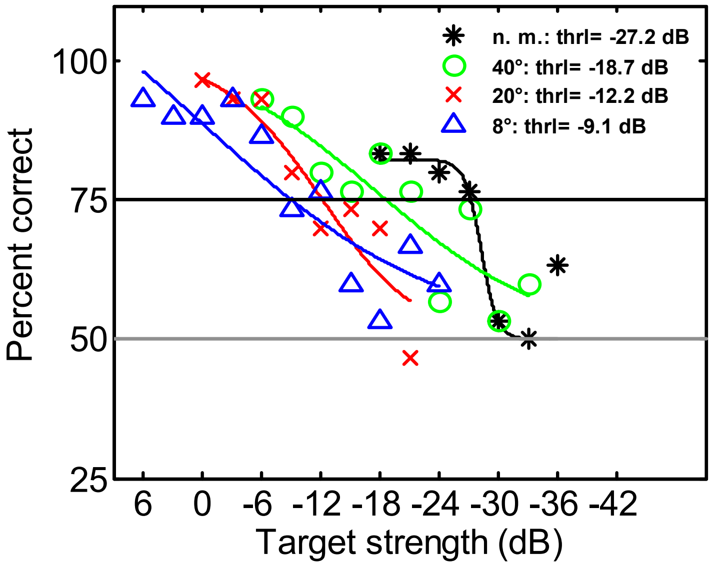

Figure 2.6: Psychometric functions for bat 3 in experiment 2
The symbols represent the percent correct choices of bat 3 in experiment 2 at different target strengths. The results for the condition without masker (black) and for the conditions with maskers at different target-masker separations are shown (40°=green, 20°=red and 8°=blue). Performance decreased with decreasing target strength. For each condition a sigmoid function (solid lines) was fitted to the data and the perception threshold (thrl) was calculated as the intersection point of the sigmoid function with the 75 % correct value (black horizontal line).

	Strength of masking (dB)				
Condition	**Bat 1**	**Bat 2**	**Bat 3**	**Bat 4**	**Bat 7**
40°	29	10	8	23	15
20°	33	18	15	20	17
8°	32	18	18	31	19

Table 2.2: Strength of masking in experiment 2
The table shows the strength of masking (dB) for each bat in experiment 2 for the three different target-masker separations (40°, 20° and 8°). To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions.

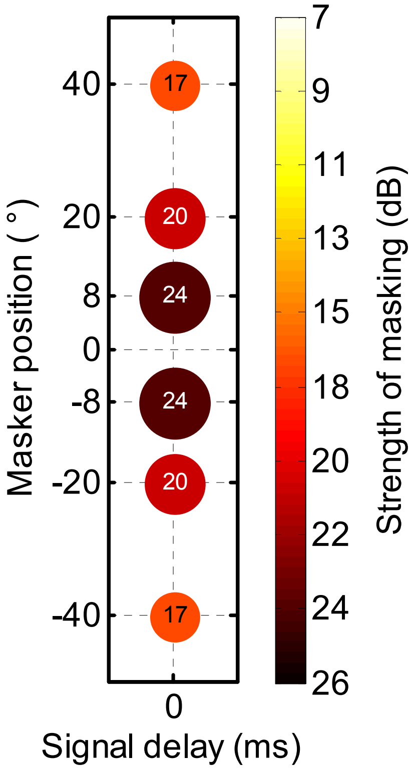

Figure 2.7: Mean strength of masking in experiment 2
The numbers as well as the color and size of the data points depict the strength of masking, averaged over all bats, in experiment 2 for the three different target-masker separations (40°, 20° and 8°). To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. To illustrate the symmetrical masking paradigm, the results have also been plotted at -8°, -20° and -40°.

2.4.1.3 Experiment 3: Spatio-temporal focus of bat sonar

In experiment 3, in which the effect of temporal separation of target and masking signals on spatial unmasking is tested, data was obtained from five bats for three different call echo delays without maskers and for eight different combinations of masker position and signal delay. The presented data is based on 14790 trials. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. The strength of masking for each individual bat is given in table 2.3. Figure 2.8 illustrates the strength of masking for the different conditions averaged over all bats. For comparison, the data points of experiment 2 are included in table 2.3 and figure 2.8.

		Strength of masking (dB)				
Condition		**Bat 1**	**Bat 2**	**Bat 3**	**Bat 4**	**Bat 7**
40°	-6 ms	28	6	10	12	5
	-3 ms	25	3	8	6	6
	0 ms	29	10	8	23	15
	3 ms	24	13	12	17	18
	6 ms	16	13	3	18	11
20°	0 ms	33	18	15	20	17
8°	-6 ms	29	10	15	21	10
	-3 ms	27	9	13	20	15
	0 ms	32	18	18	31	19
	3 ms	26	16	11	23	22
	6 ms	24	15	13	23	18

Table 2.3: Strength of masking in experiment 3

The table shows the strength of masking (dB) for each bat in experiment 3 for the presented combinations of signal delay (-6, -3, 0, 3 and 6 ms) and target-masker separations (40°, 20° and 8°). Negative signal delays indicate a backward masking situation and positive signal delays indicate a forward masking situation. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. For comparison, the data points of experiment 2 are included in table.

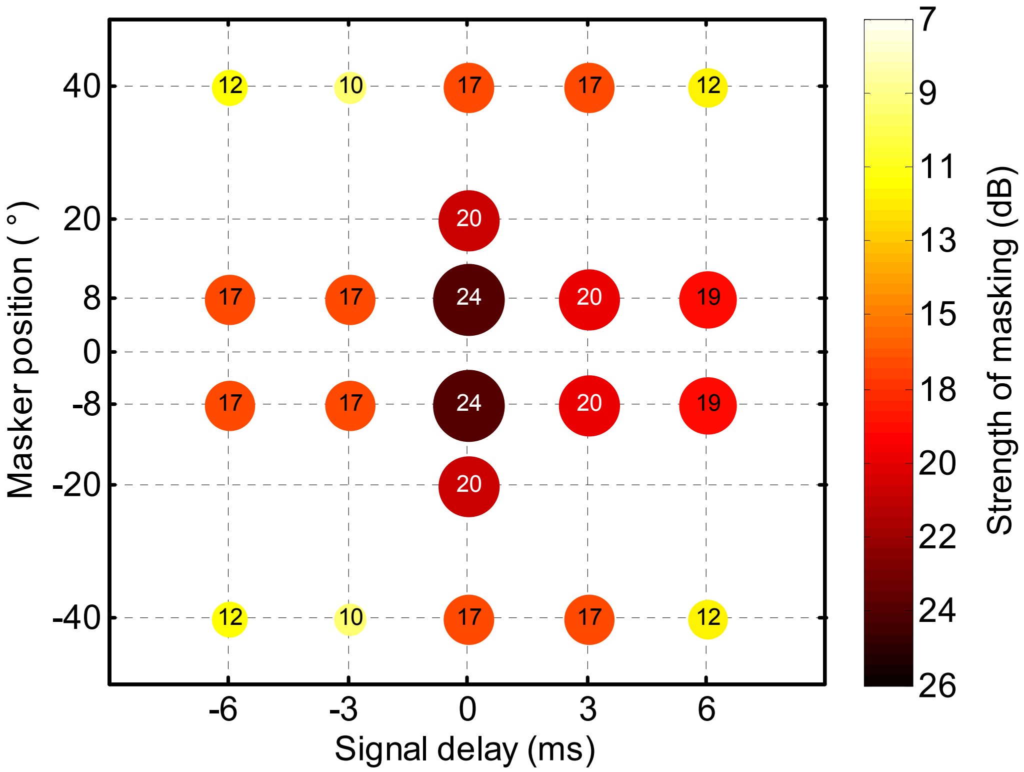

Figure 2.8: Mean strength of masking in experiment 3
The numbers as well as the color and size of the data points depict the strength of masking, averaged over all bats, in experiment 3 for the presented combinations of signal delay (-6, -3, 0, 3 and 6 ms) and target-masker separations (40°, 20° and 8°). Negative signal delays indicate a backward masking situation and positive signal delays indicate a forward masking situation. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. For comparison, the data points of experiment 2 are included in the figure. To illustrate the symmetrical masking paradigm, the results have also been plotted at -8°, -20° and -40°.

The results show a clear asymmetry between forward and backward masking. For a masker position of 40°, the strength of masking decreased by 7 dB when the target signal was played back 3 ms before the masking signals, compared to the simultaneous masking condition, while there was no release from masking when the target signal was played back 3 ms after the masking signals. Surprisingly, there was no additional release from masking when the target signal was played back 6 ms instead of 3 ms before the masking signals, but the strength of masking even increased by 2 dB. When playing back the target signal 6 ms after the masking signals, strength of masking decreased by 5 dB relative to the simultaneously masked condition. For a masker position of 8°, the release from masking was 7 dB when playing back the target signal not simultaneously with but 3 ms before the masking signals and 4 dB when playing back the target signal 3 ms after the masking signals. There was almost no additional release from masking when increasing the time interval between the target signal and the masking signals from 3 to 6 ms. Thus, forward masking was stronger than backward masking at both masker positions. When increasing the angular separation between masker and target from 8° to 40° the strength of masking decreased by 5, 7, 3 or 6 dB when the target signal was played back 6 ms before, 3 ms before, 3 ms after or 6 ms after the masking signals, respectively.

Using linear and bilinear interpolation, the results of experiments 2 and 3 can be used to create a perceptual spatio-temporal receptive field of active echolocation (fig. 2.9). To allow for a comparison between the active-acoustic and the passive-acoustic experiment, the release from masking is calculated by subtracting each value from the highest strength of masking measured in experiments 2 and 3.

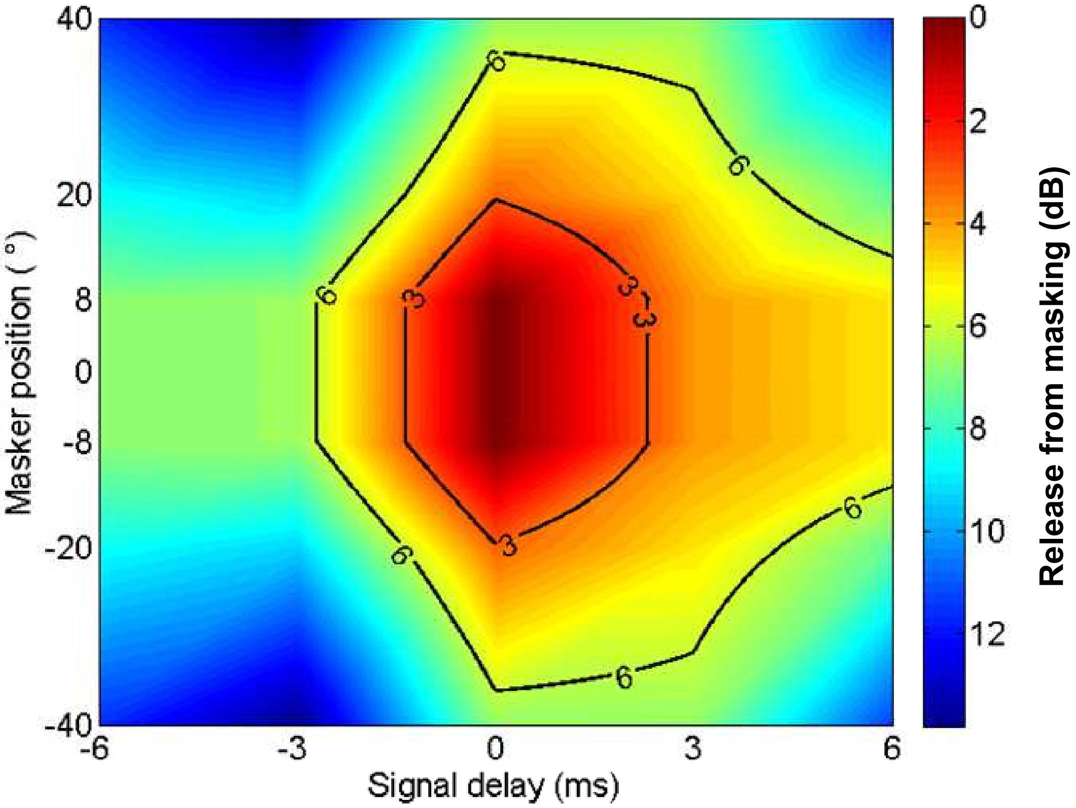

Figure 2.9: Perceptual spatio-temporal receptive field of active echolocation
In this figure, the results of experiments 2 and 3 (shown in figure 2.8) are interpolated to show the perceptual spatio-temporal receptive field of active echolocation. The release from masking is calculated by subtracting each value from the highest strength of masking measured in experiments 2 and 3. Contour lines are shown at 3 dB and 6 dB release from masking.

2.4.1.4 Experiment 4: Auditory spatio-temporal selectivity for echolocation calls

In the passive acoustic experiment, in which synthetically produced echolocation calls were presented to the bats, data was obtained from four bats for the condition without maskers and for 13 different combinations of masker position and signal delay. It is important to note, though, that not all four bats completed all experimental conditions. The results of passive auditory selectivity are based on a total of 11460 trials. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. The strength of masking for each individual bat is given in table 2.4. A summary of the strength of masking for the different conditions is shown in figure 2.10. The number of bats, that completed the experimental conditions for the corresponding signal delay, is given at the top of figure 2.10.

		Strength of masking (dB)			
Condition		**Bat 8**	**Bat 9**	**Bat 10**	**Bat 11**
40°	-6 ms		13		12
	-3 ms	8	16	7	10
	-1.5 ms		13		16
	0 ms	16	26	19	22
	3 ms		28	22	15
	6 ms		17	29	17
20°	0 ms	17	29	33	23
8°	-6 ms		18		16
	-3 ms	16	16	18	14
	-1.5 ms		17		16
	0 ms	22	31	31	22
	3 ms		33	28	21
	6 ms		28	28	17

Table 2.4: Strength of masking in experiment 4
The table shows the strength of masking (dB) for each bat in experiment 4 for the presented combinations of signal delay (-6, -3, -1.5, 0, 3 and 6 ms) and target-masker separations (40°, 20° and 8°). Negative signal delays indicate a backward masking situation and positive signal delays indicate a forward masking situation. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions.

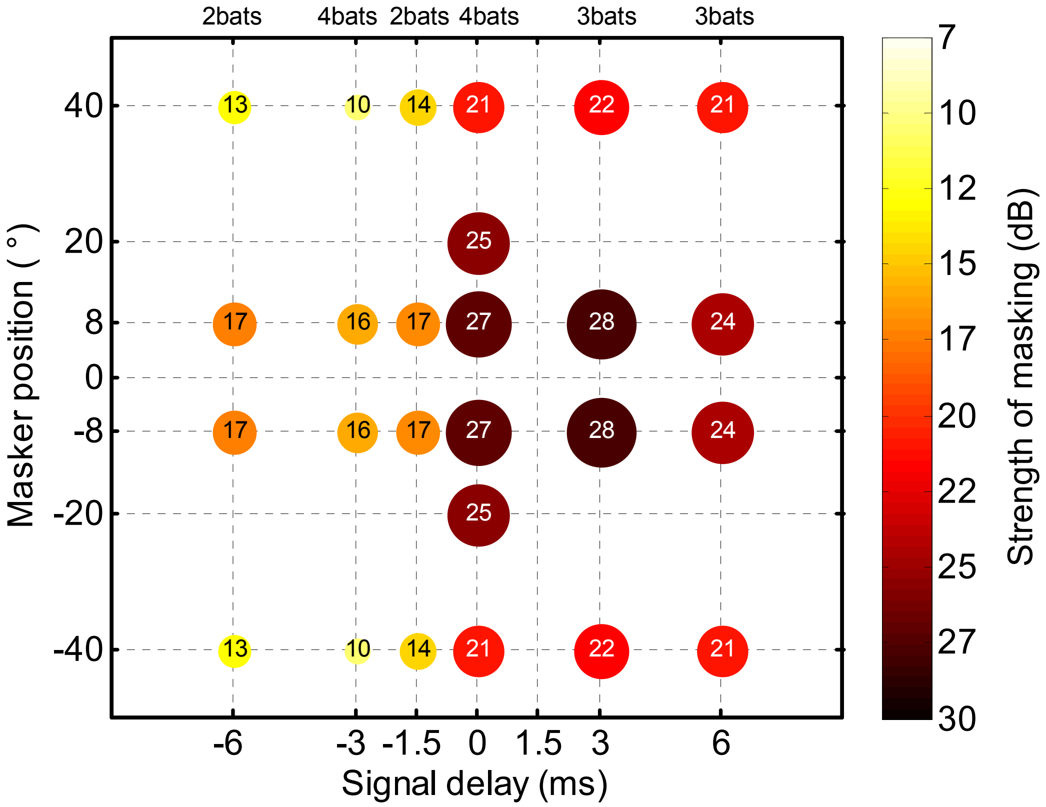

Figure 2.10: Summary of the strength of masking in experiment 4
The numbers as well as the color and size of the data points depict the strength of masking in experiment 4 for the presented combinations of signal delay (-6, -3, -1.5, 0, 3 and 6 ms) and target-masker separations (40°, 20° and 8°). Negative signal delays indicate a backward masking situation and positive signal delays indicate a forward masking situation. Please note that in this experiment not all bats have completed all conditions. The number of bats over which the results for the corresponding signal delay are averaged is given at the top of the figure. To calculate the strength of masking we subtracted the threshold of the condition without masking from the thresholds of the different masking conditions. To illustrate the symmetrical masking paradigm, the results have also been plotted at -8°, -20° and -40°.

When increasing the angular separation between target and masker from 8° to 40° the strength of masking decreased by 6 dB. As in the active acoustic experiment forward masking was much stronger than backward masking. For a masker position of 40° as well as 8°, the strength of masking decreased by 11 dB when the target signal was presented 3 ms before the masking signals compared to the simultaneous masking condition. In contrast to this, the strength of masking even increased by 1 dB for both masker positions when the target signal was presented 3 ms after the masking signals compared to the simultaneous masking condition. There was almost no additional release from masking when increasing the time interval between the target signal and the masking signals from 3 to 6 ms. When increasing the angular separation between masker and target from 8° to 40° the strength of masking decreased by 4, 5, 6 or 3 dB when the target signal was played back 6 ms before, 3 ms before, 3 ms after or 6 ms after the masking signals, respectively.

Using linear and bilinear interpolation, the results of experiment 4 can be used to create a perceptual spatio-temporal receptive field of passive hearing (fig. 2.11). To allow for a comparison between the active-acoustic and the passive-acoustic experiment, the release from masking is calculated by subtracting each value from the highest strength of masking measured in experiment 4.

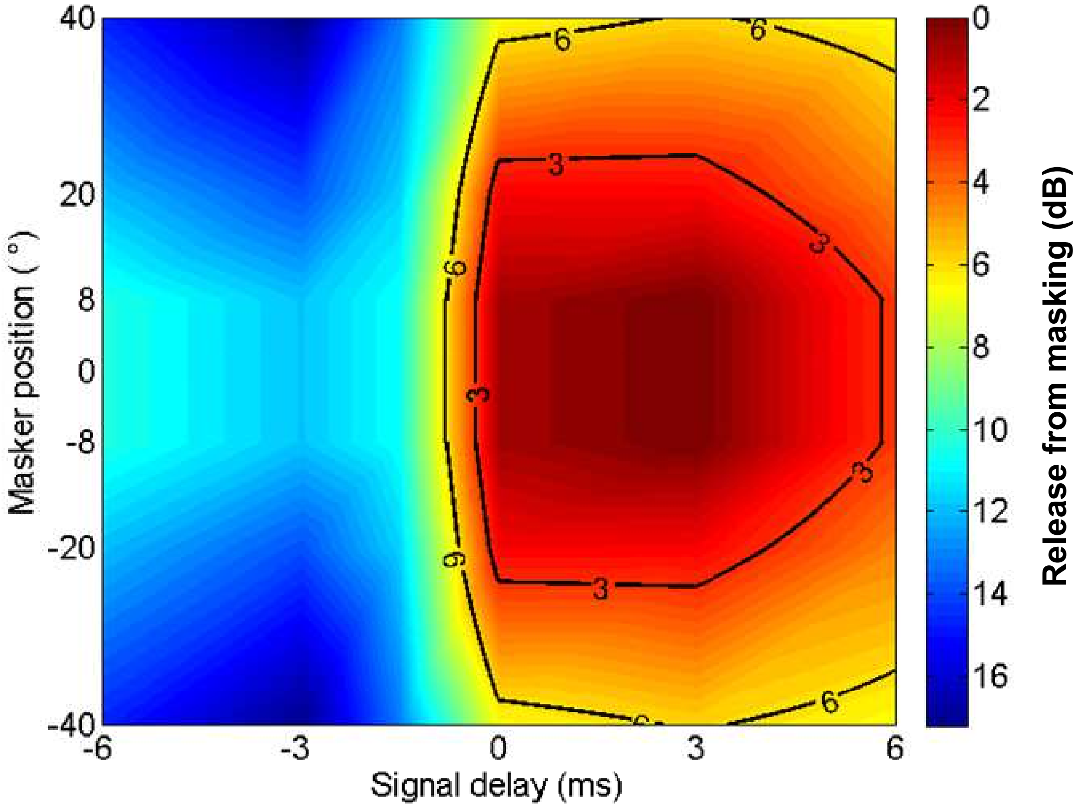

Figure 2.11: Perceptual spatio-temporal receptive field of passive hearing
In this figure, the results of experiment 4 (shown in figure 2.10) are interpolated to show the perceptual spatio-temporal receptive field of passive hearing. The release from masking is calculated by subtracting each value from the highest strength of masking measured in experiment 4. Contour lines are shown at 3 dB and 6 dB release from masking.

2.4.2 Sound analysis

We analyzed the echolocation calls that the bats emitted in experiment 1. Figure 2.12 shows an example echolocation call for each bat.

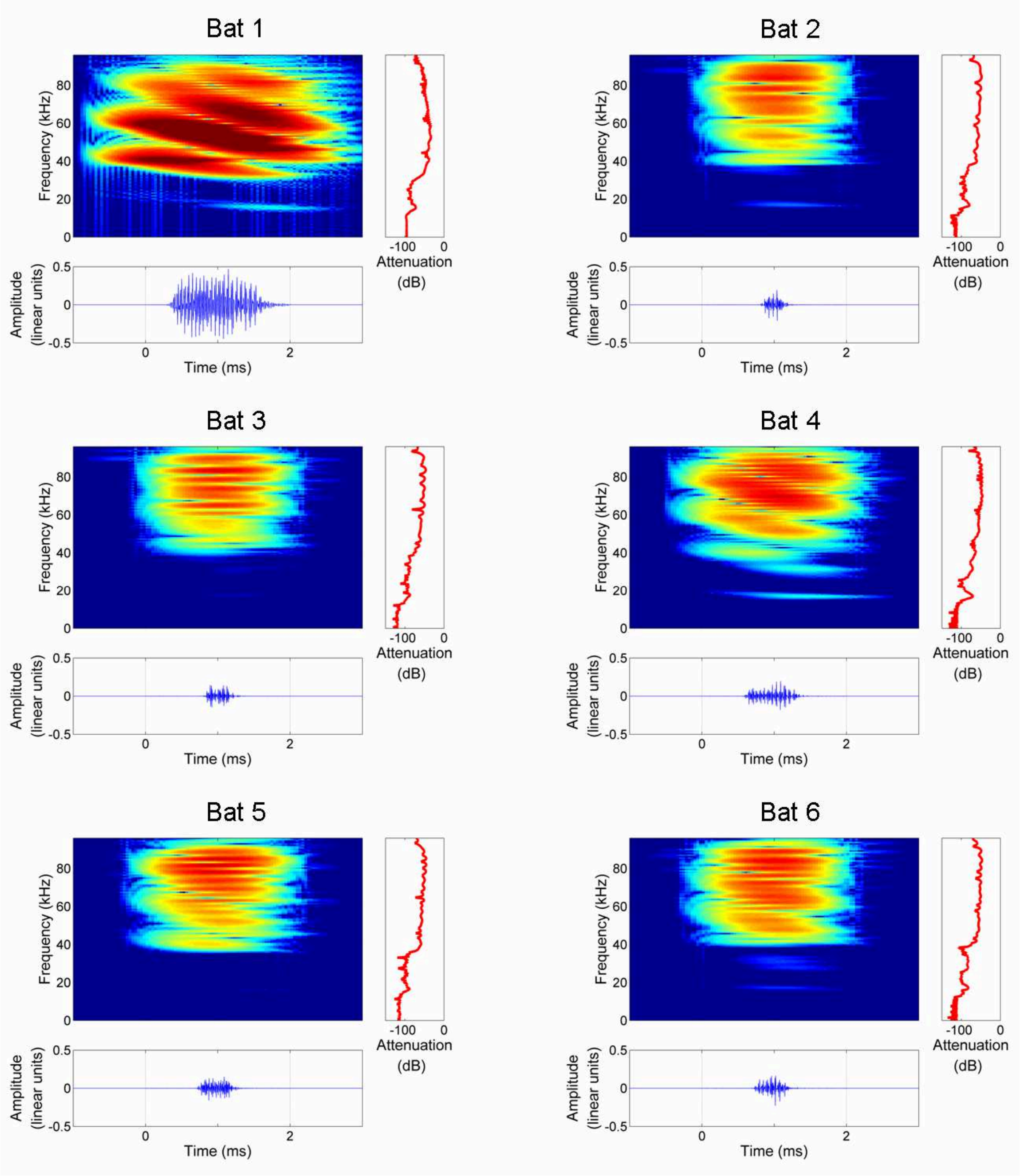

Figure 2.12: Example echolocation calls
The figure shows one example call of each bat as spectrogram (top, left), as amplitude spectrum (top, right) and as oscillogram (bottom).

2.4.2.1 Directionality analysis

The directionality of the echolocation calls, averaged over all bats, is illustrated in figure 2.13. The analysis is based on 13732 calls from bat 1, 16103 calls from bat 2, 9753 calls from bat 3, 6337 calls from bat 4, 10530 calls from bat 5 and 5889 calls from bat 6. The -6 dB (-3 dB) angle of the emission curve was 24° (16°) for the broadband call, 54° (37°) when filtered around the 2nd harmonic and 22° (15°) when filtered around the 4th harmonic. The directionality of the broadband calls is shown for each bat individually in figure 2.14.

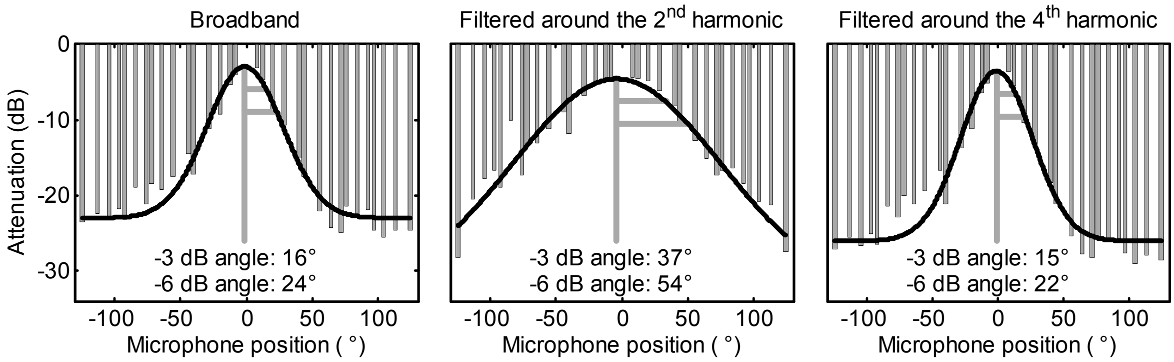

Figure 2.13: Directionality of the echolocation calls
The directionality of the broadband call (left), the call filtered around the 2nd harmonic (middle) and the call filtered around the 4th harmonic (right) are depicted. The grey bars show the measured levels at the 33 different spatial positions. The directionality of the calls is calculated by fitting a Gaussian (black curve) to the data and determining the angle at which the Gaussian is 3 or 6 dB below its peak. The analysis is based on 13732 calls from bat 1, 16103 calls from bat 2, 9753 calls from bat 3, 6337 calls from bat 4, 10530 calls from bat 5 and 5889 calls from bat 6.

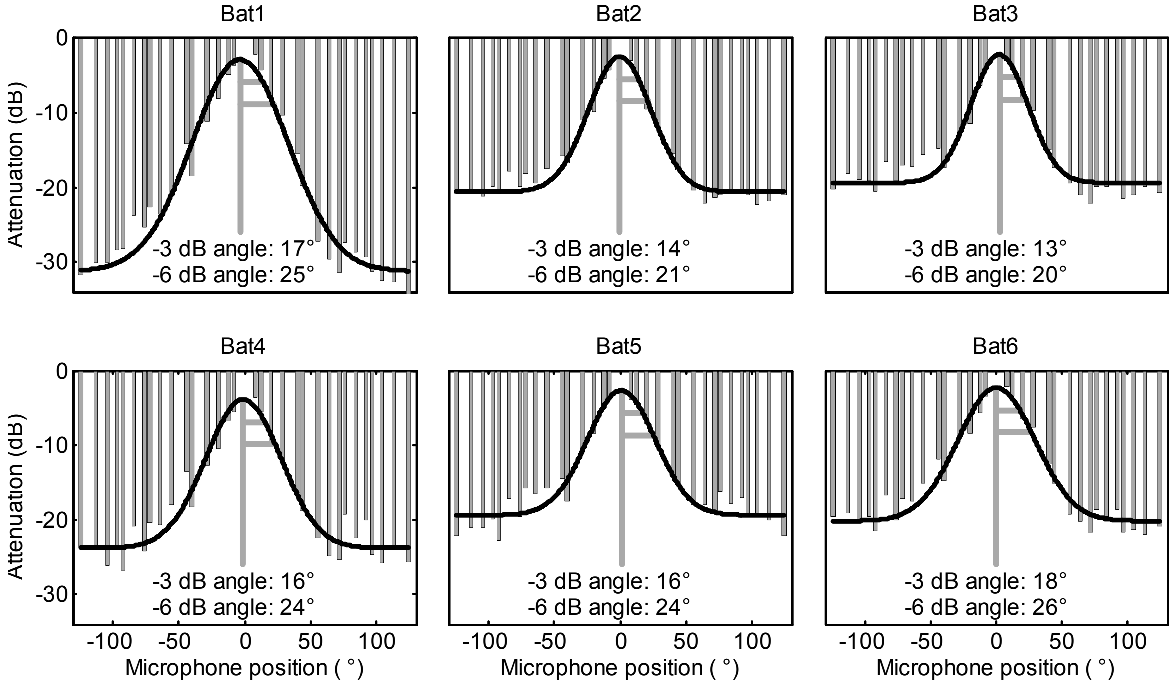

Figure 2.14: Directionality of the broadband echolocation calls for each bat
The directionality of the broadband echolocation calls is depicted for each bat. The grey bars show the measured levels at the 33 different spatial positions. The directionality of the calls is calculated by fitting a Gaussian (black curve) to the data and determining the angle at which the Gaussian is 3 or 6 dB below its peak. The analysis is based on 13732 calls from bat 1, 16103 calls from bat 2, 9753 calls from bat 3, 6337 calls from bat 4, 10530 calls from bat 5 and 5889 calls from bat 6.

2.4.2.2 Spectral analysis

We also conducted a spectral analysis of the bats' echolocation calls emitted in experiment 1. The median best frequency, the median frequency cetroid and the median fundamental frequency are summarized in table 2.5. The analysis is based on 28427 calls from bat 1, 27107 calls from bat 2, 16055 calls from bat 3, 15367 calls from bat 4, 19648 calls from bat 5 and 10924 calls from bat 6.

	Median (kHz)					
	Bat 1	**Bat 2**	**Bat 3**	**Bat 4**	**Bat 5**	**Bat 6**
Best frequency	76.1	73.5	83.3	84.0	75.8	75.8
Frequency centroid	64.7	69.6	72.2	69.9	69.6	69.2
Fundamental frequency	19.2	19.7	19.7	20.2	19.2	19.2

Table 2.5: Spectral analysis
The median values for the best frequency, the frequency centroid and the fundamental frequency of the echolocation calls in experiment 1 are given in kHz for each bat. The analysis is based on 28427 calls from bat 1, 27107 calls from bat 2, 16055 calls from bat 3, 15367 calls from bat 4, 19648 calls from bat 5 and 10924 calls from bat 6.

2.4.3 Simulation

The results of the simulation of our experiments are shown in figure 2.15. For an increase of the angular separation between target and masker from 7.5 to 40°, the simulation predicts a release from masking by 10 dB for the active acoustic condition and by 3 dB for the passive acoustic condition.

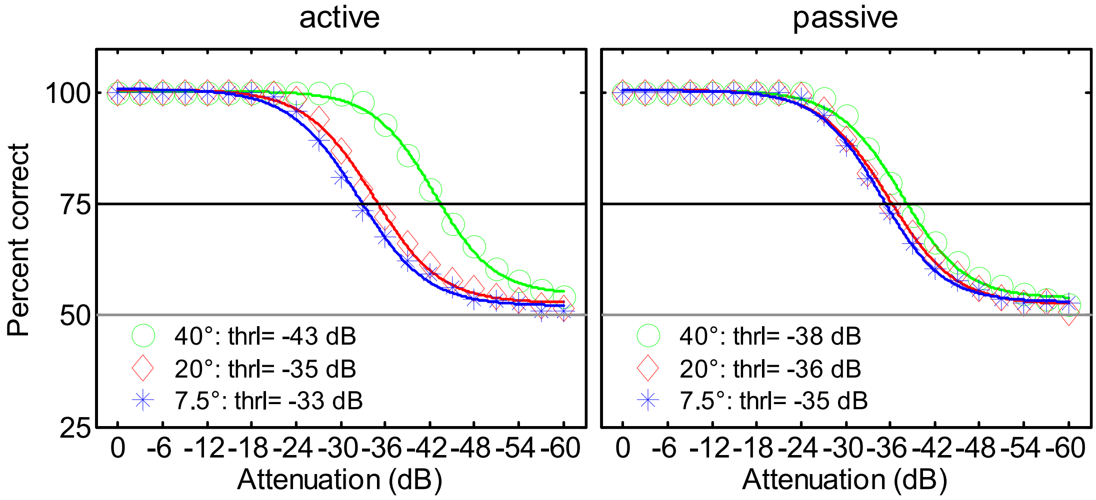

Figure 2.15: Results of the simulation of the experiment about the spatial focus of *P. discolor*'s echolocation system
We simulated the active-acoustic (left) as well as the passive-acoustic experiment (right). The symbols represent the percent correct choices calculated in the simulation at different target signal attenuations. The results for three different masking conditions are shown (target-masker separations: 40°=green, 20°=red and 8°=blue). Performance decreased with decreasing target strength. For each condition a sigmoid function (solid lines) was fitted to the data and the perception threshold (thrl) was calculated as the intersection point of the sigmoid function with the 75 % correct value (black horizontal line).

2.5 Discussion

2.5.1 Summary and discussion of results

We investigated the spatio-temporal focus of bat sonar in the bat *P. discolor* in a series of formal psychophysical phantom target experiments. In the active-acoustic experiment, in which the bats had to evaluate the echoes of their own echolocation calls, an increase of the angular separation between target and masker from 8° to 40° led to a decrease of the strength of masking by 7 dB. The same result was obtained in the control experiment in which we implemented a triggered playback to prevent the bats from listening to passive acoustic background noise that might be generated by the microphone preamplifier. This confirms that the bats in the active-acoustic experiment really solved the task by listening to the echoes of their echolocation calls. If the maskers were at the same position as the target in the simultaneous masking condition, the bats could only rely on echo intensity differences to solve the task. Heinrich *et al.* (2011) showed that *P. discolor* requires echo-intensity differences of 5 dB to discriminate a fainter from a louder echo. In our active-acoustic experiment the level of the signal side is about 6 dB higher than the level of the standard side when the target-masker separation is set to 8° and the target signal is presented at threshold level. Thus, no spatial unmasking is expected for an increase of target-masker separation from 0° to 8°.

In the passive-acoustic experiment the bats had to evaluate artificially produced echolocation calls that were independent of the bats' own echolocation activity. When increasing the angular separation between target and masker from 8 to 40° in this experiment, the strength of masking deceased by 6 dB. By conducting an active- and a passive-acoustic experiment we were able to analyze to which extent the bats' emitting system and to which extend the bats' receiving system contribute to the spatial sensitivity of bat sonar. Surprisingly, the release from masking for an increase of target-masker separation from 8 to 40° was only 1 dB stronger in the active-acoustic than in the passive-acoustic experiment. This indicates that the directionality of the emitting system contributes only very little to the directionality of the whole echolocation system in *P. discolor*. Based on the results of our simulation on the other hand, we would expect that the release from masking for an increase of target-masker separation from 7.5 to 40° is 7 dB stronger in the active- than in the passive acoustic experiment. When regarding the spatial sensitivity patterns of *P. discolor*'s emitting system simulated by Vanderelst (2010), a main lobe and two side lobes are apparent for high frequencies. The notches between the main lobe and the side lobes are located at a horizontal position close to ± 40°. This leads to a strong spatial unmasking in the simulation of our active-acoustic experiment for a masker-target separation of 40°. An important difference between the simulation and our experiments is that the bats constantly moved their ears during the experiments while we used a static HRTF for the simulation. The time-variant spatial receptive field of the bats' receiving system that can be focused on the target of interest might enhance the bat's spatial sensitivity especially in a passive-acoustic experiment. Furthermore, for a target-masker separation of 40°, the two central maskers were positioned side by side, directly in front of the bat. In case that the bat directed some of its echolocation calls towards the two maskers instead of towards the right or the left target, the target detection would be more difficult.

While there is already a considerable release from masking in the active-acoustic experiment when the angular separation between target and masker is increased from 8 to 20°, in the passive-acoustic experiment most of the measured spatial unmasking seems to be achieved when the target-masker separation is increased from 20 to 40°. This indicates that especially at small angular separations the bats' spatial resolution is better in the active than in the passive condition.

In the active-acoustic as well as in the passive-acoustic experiment the strength of masking decreased when the target signal was temporally separated from the masking signals compared to the simultaneous masking situation. A clear asymmetry between forward and backward masking can be seen: In the active-acoustic experiment the strength of masking decreased by about 7 dB when the target signal preceded the masking signal by 3 ms but only by about 2 dB when the target signal followed the masking signal after 3 ms. In the passive-acoustic experiment the strength of masking decreased by about 11 dB when the target signal preceded the masking signal by 3 ms and even increased by about 1 dB when the target signal followed the masking signal after 3 ms.

Forward masking was stronger in the passive- than in the active-acoustic experiment. This means that the asymmetry of backward and forward masking is less pronounced in active echolocation than in passive hearing. The results indicate that the use of active echolocation leads to a temporal sharpening of the spatio-temporal receptive field of *P. discolor*. This can be seen clearly when comparing figure 2.9 and figure 2.11.

The half amplitude angle of the bats' emissions was 54° when filtered around the 2nd harmonic and 22° when filtered around the 4th harmonic. The echolocation calls of the bats had most energy in the fourth or even the fifth harmonic. Bat 1 also sometimes emitted calls that had most energy in the third harmonic. The frequency centroid of the calls was at about 70 kHz and the median fundamental frequency was about 19.5 kHz.

2.5.2 Comparison of the emission pattern

Many studies have investigated the directionality of echolocation calls. Vanderelst *et al.* (2010) simulated the emission pattern of *P. discolor*. The results show half-amplitude angles of about 50° lateral at 40 kHz and of about 30° lateral at 80 kHz. These results agree well with the directionality of the bats' echolocation calls measured in this study (54° when filtered around 38 kHz and 22° when filtered around 76 kHz). Studies in which the directionality of echolocation calls was measured in the laboratory for various bat species also report half-amplitude angles in the range of about 25° to 60° (Shimozawa *et al*. 1974; Schnitzler & Grinnell 1977; Mogensen & Møhl 1979; Henze & Oneill 1991; Ghose & Moss 2003; Hiryu *et al*. 2006). It is surprising that the bats in the current study emitted calls with only an average directionality even though they would have benefited strongly from increasing the directionality of their echolocation calls. One factor might be that because of the sampling frequency of our audio device (192 kHz) we were not able to take frequencies above 96 kHz into account. *P. discolor* might be able to emit calls with a higher directionality by increasing the energy content in the fifth harmonic. As the fifth harmonic of the calls of *P. discolor* contains frequencies above 96 kHz, this potential increase in directionality would not be visible in our directionality analysis. Surlykke *et al*. (2009) showed in *M. daubentonii* that bats emit echolocation calls with a much higher directionality in the field than in the laboratory (half-amplitude angle of 20° instead of 40°). Thus, *P. discolor* might also emit calls with a higher directionality in the field than in the current study.

2.5.3 Comparison with other spatial unmasking experiments

As mentioned in the introduction, Sümer *et al.* (2009) investigated spatial unmasking in the bat *E. fuscus* in a real target 2AFC paradigm. The authors measured a complete release from masking (of 29.4 dB) for an angular separation of 23° between target and masker. In contrast to this, we did not measure a complete release from masking even when target and maskers were separated by 40°. An important difference between the two studies is that the target in the study of Sümer *et al.* (2009) was only flanked by one masker while the target in our experiments was symmetrically surrounded by two maskers. It has been shown for speech recognition tasks in humans that spatial separation effects are weaker in situations in which speech (that is presented from straight ahead) is masked by two noise sources arranged symmetrically around the target than in situations in which a speech signal is only masked by one noise source (reviewed in Bronkhorst 2000). This difference in spatial separation effects can be explained by the better ear effect: When only one masker is present, the overall loudness of this masker is reduced at the contralateral ear due to the head shadow effect. This difference between better and worse ear performance is no longer available in symmetrical masking situations (Bronkhorst & Plomp 1992; Bronkhorst 2000; Noble & Perrett 2002). This might also partly explain the stronger spatial unmasking effect in the study of Sümer *et al.* (2009) compared to our study. In contrast to the experiments in humans, the bats in the study of Sümer *et al.* and in our experiment could move their head and ears to shift their auditory receptive field such that they obtain an optimal signal to noise ratio. This effect can be intensified by additionally adjusting the aim of the sonar beam. Thus, when only one masker is present the bats can profit from off-space listening. Only in a symmetrical masking situation the bats are forced to center their perceptual receptive field at the target to obtain the best signal to noise ratio (figure 2.16). This is another reason for the stronger spatial unmasking effect in the study of Sümer *et al. (2009).*

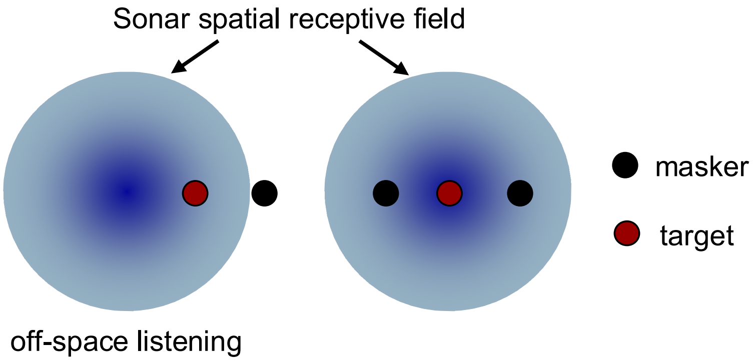

Figure 2.16: Illustration of off-space listening
When a target (red point) is masked by only one masker (black point) bats can improve their target detection performance by directing their sonar spatial receptive field (blue circle) to the side where no masker is present. This is called off-space listening (left). In a symmetrical masking situation the bats are forced to center their sonar spatial receptive field at the target to obtain the best signal to noise ratio (right).

A comparison of our spatial unmasking results with the results obtained in studies in humans, where a speech signal was masked by two symmetrically arranged maskers, has to be handled with care because these results strongly depend on the particular masking signals which are very different from those used in our study. In the study of Noble and Perrett (2002) subjects hat to follow a target speech signal in the presence of two masking signals that were either located at the same position or were displaced symmetrically by 30° relative to the speech signal. The benefit from spatial separation was 2.4 dB for the use of correlated noise as a masking signal, 0.4 dB for uncorrelated noise and 5 dB for speech. Bronkhorst and Plomp (1992) used two independently fluctuating speech-shaped noise sources as symmetrically arranged maskers and found a separation benefit of 4.6 dB for a target masker separation of 90° compared to a situation where the maskers were co-located with the speech source. In a study that Binetti conducted in the Wiegrebe lab (Binetti 2009) subjects had to detect a noise signal, that was band-pass filtered around 500, 1000, 2000, 4000 or 8000 Hz, in the presence of two symmetrically arranged maskers. The maskers consisted of uncorrelated noise with a spectral notch around the frequency of the target signal. No spatial unmasking effect was measured in this study up to angular separations between target and masker of 90°. For an increase of angular separation between target and masker from 8 to 40° we measured a spatial unmasking effect of 7 dB in the active- and of 6 dB in the passive-acoustic experiment of this study. Thus, although a comparison has to be handled with care, bats seem to experience stronger spatial unmasking than humans. Bats might have a higher spatial selectivity because they usually analyze ultrasonic sounds with wavelengths that are relatively short compared to the size of their pinnae. Furthermore, bats can actively position their pinnae and direct their echolocation beam to focus on a target of interest.

When comparing the spatial unmasking experiments in humans with the current experiments it is important to keep in mind that the signals used in the studies are fundamentally different. In the current study, target and masker signals are partially coherent in the active-acoustic paradigm, or even fully coherent in the passive-acoustic paradigm. Target and masker signals are only partially coherent in the active-acoustic paradigm because sounds emitted by a bat do not spread equally in all directions but are focused in the forward direction. When two coherent sounds arrive almost simultaneously at the ears from different directions a psychophysical phenomenon called the ‘precedence effect’ has been observed in humans (reviewed in Blauert 1997), cats (reviewed in Dent *et al*. 2005), rats (Kelly 1974), fur seals (Babushina & Polyakov 2001), birds (e.g. Dent & Dooling 2004) and crickets (Wyttenbach & Hoy 1993). The precedence effect is relevant to sound localization in reverberant environments. It describes the psychophysical phenomenon that the position of a sound source is mainly determined by the directional information of the direct (and first) sound, while the directional information of the echoes (that arrive later) is suppressed. Depending on the time interval between the leading and the lagging sound the precedence effect can be subdivided into three phenomena: For time intervals between 0 and 1 ms ‘summing localization’ occurs and instead of perceiving two individual spatially separated sound sources the subjects perceive a “phantom” sound source located midways between the sources. For time intervals between about 1 and 5 ms ‘localization dominance’ occurs and the auditory image is perceived close to the position of the leading sound, while the directional information of the lagging sound is suppressed. When the interval between the leading and the lagging sound is increased further, two separate sound events are perceived (for reviews, see: Blauert 1997; Litovsky *et al*. 1999; Dent *et al*. 2005). This means that, according to the precedence effect, the two masking signals would perceptually fall onto the location of the target signal in our experimental paradigm. Thus, if bats showed summing localization as e.g. humans do, no spatial release from masking would be expected in our passive-acoustic experiments. In contrast to humans, bats rely on the spatial information of echoes for orientation and navigation. Bats also perceive higher order echoes, when an echo is reflected from a second object. Thus, bats might be able to suppress the spatial information of higher order echoes. Schuchmann *et al*. (2006) showed that *P. discolor* does not generally show spatial echo suppression. However, they also discuss that bats might be able to suppress the spatial information of higher order echoes in situations in which it is beneficial for them to do so. Furthermore, two studies revealed a possible neural correlate of a precedence effect in bats (Burger & Pollak 2001; Pollak *et al*. 2002). Thus, bats might be able to recruit localization dominance if needed. However, for orientation and navigation bats depend on the spatial information contained in the echoes and in accordance with that *P.discolor* did not show spatial echo suppression in the study of Schuchmann *et al.* (2006). Thus, it is unlikely that the bats used summing localization in the current study as this strategy would be very disadvantageous for them.

2.5.4 Comparison with other temporal unmasking experiments

There are also several studies in which non-simultaneous masking in bats was investigated. When *E. fuscus* had to detect a virtual sonar target in the presence of masking noise, masking was only observed if the masker was delayed by less than 2 ms (Møhl & Surlykke 1989). Backward masking was also measured when an angular masker was positioned less than 20 cm behind a wire (corresponding to an echo delay of 1.2 ms) (Sümer *et al*. 2009). Moss *et al.* (2006) observed that the insect capture success rate of *E. fuscus* was reduced when the insect was 40 cm or less from the clutter (corresponding to an echo delay of 2.3 ms). Capture success was also described to decrease when *Myotis nattereri* attacked mealworms attached closer than 20 cm (echo delay of 1.2 ms) to an artificial hedge (Pflästerer 2007) or when *Eptesicus nilssonii* hunted moths flying lower than 50 cm (echo delay of 2.9 ms) over a field (Rydell 1998). Simmons *et al.* investigated backward and forward masking in *E. fuscus* and found that masking only takes place when target and masker echoes are separated by less than 0.5 ms (Simmons *et al*. 1988; Simmons *et al*. 1989). In contrast to this, Møhl (1986) measured a strong masking effect in *Pipistrellus pipistrellus* when a real echo preceded a phantom target by 3 ms and Hatley (1992) even observed a masking effect in *E. fuscus* and in *Noctilio leporinus* when a virtual echo was followed by a real echo after 6 ms. In an electrophysiological study, Lu and Jen (2002) investigated masking in neurons in the inferior colliculus of *E. fuscus*. On average, masking occurred at masker delays between about -6 ms (forward masking) and 0.5 ms (backward masking). In some cases masking has even been observed for masker delays between -10 and 4 ms. In the current study we did not measure a complete release from masking in *P. discolor* even when the masking echoes arrived 6 ms before or 6 ms after the target echo at the bat’s ear. In contrast to the studies mentioned above, each target in our study was masked by two maskers and not by one and the target and masker echoes were not only separated temporally but also spatially. Interestingly, the effect of spatial unmasking was still present even when target and masker echoes were temporally separated. We also observed that the effect of forward masking was much stronger than the effect of backward masking for the respective time intervals. This so called asymmetry of non-simultaneous temporal masking has also been shown in other studies in humans (Raab 1961; Babkoff & Sutton 1968; Wilson & Carhart 1971; Feth & Omalley 1977; Oxenham & Moore 1994), parakeets (Dooling & Searcy 1980) and bats (Faure *et al*. 2003).

2.5.5 Conclusion and outlook

We developed an experimental paradigm to measure the spatio-temporal focus of bat sonar in *P. discolor*. Our results indicate that the spatial selectivity of the whole echolocation system is mainly determined by the spatial selectivity of the receiving system. The bat's pinnae which are relatively big compared to the wavelengths of the analyzed sounds and which are constantly in motion might constitute a highly directional filter. However, the contribution of the emitting system might be higher in the field than in our laboratory experiments as bats have been shown to emit much more directional echolocation calls in the field than in the laboratory (Surlykke *et al*. 2009). Our results indicate that the use of active echolocation leads to a temporal sharpening of the spatio-temporal receptive field of *P. discolor*. It will be interesting to investigate the spatio-temporal focus of bat sonar in a more natural situation and to compare the results of this study with electrophysiologically measured spatio-temporal receptive fields.

3 What’s the buzz? Sensory-motor coupling during high-speed echolocation in bats

Cornelia Geberl*, Signe Brinkløv*, Lutz Wiegrebe and Annemarie Surlykke

*shared first authorship

This project was conducted in close collaboration with Signe Brinkløv and Annemarie Surlykke, University of Southern Denmark. Annemarie Surlykke and Signe Brinkløv designed the laboratory experiments. Data collection and analysis of raw data for the laboratory experiments was done by Signe Brinkløv. Lutz Wiegrebe and I designed the field experiments and the data analysis. Thomas Dera customized the EyeSeeCam program (Schneider et al. 2009) to implement a real time positioning of bats for the field experiments. I collected as well as analyzed the data of the field experiments and conducted all statistical analysis. Marc Sieber assisted me in the data collection for the field experiments. Figures 3.2 and 3.5 were designed by Singe Brinkløv while the remaining figures were designed by me. The manuscript was written by Annemarie Surlykke, Signe Brinkløv, Lutz Wiegrebe and me. A revised version of this manuscript, in which figures 3.4, 3.6, 3.9 and 3.11 will be excluded, will be submitted to PNAS.

3.1 Abstract

Biosonar is one of the few truly active senses in the animal kingdom: bats and toothed whales image their surroundings through auditory analysis of self-generated transient sound signals. This stroboscopic active sensing, however, presents a challenge for fast reactions to transient changes in the environment because between sonar emissions, the animal moves effectively ‘senseless’ in the dark. Presumably to meet this challenge, insectivorous bats and toothed whales produce a terminal buzz during the last phase of prey pursuit, with emission rates up to 200 Hz or 700 Hz, respectively.

Here we address, in a combined flight room and field study, how fast the echolocating bat *Myotis daubentonii* can react to such sudden changes occurring during the terminal buzz. Specifically, we removed the prey, suspended either in air or on a water surface, at different times before expected bat-prey contact. Our results show that the bats shortened the terminal buzz even when prey was removed within the last 100 ms (about 30 cm) before expected contact; and the movement program is changed even when the prey is removed immediately before expected contact.

These data show that the motor programs underlying the extremely fast vocalization rates and body movements during the last phase of bat prey capture are not stereotyped but continually dynamically adapted in response to sensory feedback. The bats’ reaction time for this complex behavior was about 100 ms. As reaction times for other complex multi-stage behaviors in completely different systems tend to be longer, bats seem to overcome the problem of stroboscopic active sensing by emitting echolocation calls at a very high rate during the terminal buzz.

3.2 Introduction

All of our senses sampling space beyond our reach are passive, i.e. they rely on external energy like light, sound, or touch, to stimulate a sensory receptor. Active senses, where the animal itself produces the energy to sample the environment, are rare in the animal kingdom. They comprise vision of some deep-sea fish (Denton *et al*. 1970; Oday & Fernandez 1974; Somiya 1982; Denton *et al*. 1985; Partridge & Douglas 1995), the active electric sense by weakly electric fishes (for reviews, see Carr 1990; Assad *et al*. 1999; Bullock *et al*. 2005) and echolocation, i.e. sensing of the environment through the auditory analysis of self-generated sounds (Griffin 1958; Neuweiler 2000). Advanced echolocation, which is found in bats and toothed whales, involves dynamic adaptation of the outgoing sound and behavior, e.g. head aim and flight path, based on perception of the surroundings through auditory processing of the information carried by returning echoes.

There is a great variation in echolocation signals across echolocating predators, but the temporal pattern during prey pursuit, consisting of a search, approach and terminal phase, is rather stereotyped, be it a bat hunting flying insects in air or over water (Griffin 1958; Simmons *et al*. 1979), or a toothed whale hunting for fish (Miller *et al*. 2004; Johnson *et al*. 2006; DeRuiter *et al*. 2009). Specifically, the repetition rate of the transient echolocation calls increases dramatically during the terminal phase of prey pursuit and all data so far show buzzes to be universally present in the acoustic behavior of echolocators capturing moving prey, be it bats or whales. Repetition rates during odontocete buzzes reach up to 640 Hz in porpoises and, in contrast to echolocating bats, buzzes usually continue beyond the first prey contact, often even beyond the end of prey handling (DeRuiter *et al*. 2009). The terminal buzz in many vespertilionid and molossid bats can be subdivided into a buzz 1 and a buzz 2 phase. Buzz 2 is characterized by a constant high repetition rate and a characteristic drop in frequency of up to an octave (Griffin *et al*. 1960; Simmons *et al*. 1979; Kalko & Schnitzler 1989; Neuweiler 1989; Mora *et al*. 2004; Guillen-Servent & Ibanez 2007). The trawling Daubenton's bat, *Myotis daubentonii,* produces laryngeal calls at a repetition rate of 180-200 Hz during the terminal buzz (Kalko & Schnitzler 1989). Recent work has shown that super-fast laryngeal muscles have evolved in bats to allow for these exceptionally fast vocalization rates (Elemans *et al*. 2011).

Despite intensive studies of the function of the terminal buzz, it is still not understood in detail and subject to much debate. It has been hypothesized that the buzz in odontocetes not only functions to guide the whale to its prey through a high update rate on prey position

(Johnson *et al*. 2006), but may also serve to track potentially escaping prey (DeRuiter *et al*. 2009). For bats, Schnitzler and Kalko (2001) argue that the short broadband call design of the terminal buzz, which is quite similar among insectivorous bats, is optimized for target localization and the extremely high call repetition rates are well suited for tracking and adjusting to fast target movement. Emitting a buzz might also guide bats to a safe landing by allowing for a rapid update of distance information (Russo *et al*. 2007). In contrast, Melcón *et al.* (2007) argue that feedback from buzz 2 cannot be used to guide the bat to the prey or landing site because it reaches the bat too late. Buzz 2 starts around 50 ms before contact in landing or hunting in *Myotis nattereri* and *Myotis myotis* and this time corresponds approximately to the estimated reaction time. Instead they reason that the function of Buzz 2 is to provide the bat with post capture or landing information that may help to assess the cause of unsuccessful attempts and to eventually react adequately.

Here we aimed to quantify on a behavioral level the effect of very fast sensory feedback on motor control of vocal and capture behavior during the terminal buzz. We did this by a combination of flight room and field experiments on our model species, *M. daubentonii*, where we removed the prey at specific times down to a few milliseconds before expected prey contact during pursuit sequences. We assessed the effect by analyzing changes in the bats' temporal sonar emission pattern and capture movements relative to control conditions without prey removal.

3.3 Materials and methods

3.3.1 Aerial captures in the field

3.3.1.1 Recording sites

Fieldwork took place from April to October in 2010 and 2011 at two different recording sites along the river Würm, one in Munich-Pasing (48° 8'1.57"N/11°26'53.94"E) and one in Planegg (48° 6'18.16"N/11°25'23.35"E). The distance between the two recording sites was 4-5 km, making it highly unlikely that we recorded from the same bat at both sites. We trained wild Daubenton's bats (*M. daubentonii*), probably one individual in each place, to take prey suspended from a string by first dispersing mealworms (*Tenebrio molitor)* on the water surface and later offering a mealworm attached to a string directly on the water surface, gradually elevating the worm above the river surface to a height of about 40 cm. Once the bats were frequently attacking the presented mealworm, they were monitored with synchronized high-speed video and audio recordings during their approach and capture of the tethered mealworms. In a subset of trials, the tethered prey was instantaneously removed when the distance between the bat and the tethered prey decreased below a critical value and the bat's flight and vocal behavior was recorded.

3.3.1.2 Experimental setup

Mealworms were suspended from a nylon thread (Ø 0.15 mm) hanging from a fishing rod which was anchored to an aluminum pillar on the river bank. The tip of the fishing rod was bent towards the ground with a taut fishing line (Ø 0.25 mm) spanning from the tip of the fishing rod to a lifting solenoid mounted at the pillar (fig. 3.1). When the solenoid was activated, the fishing line was loosened, releasing the tip of the fishing rod and instantaneously flinging the mealworm upwards.

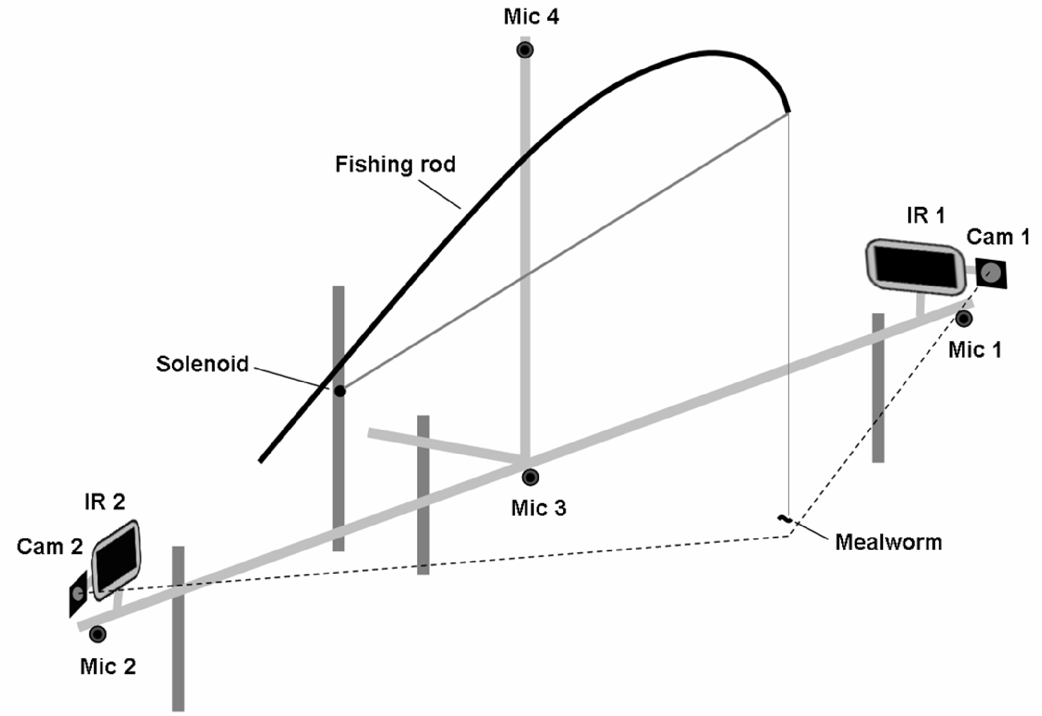

Figure 3.1: Field setup
The figure shows a schematic of the field setup. Mealworms were suspended form a nylon thread hanging from a fishing rod. The fishing rod was put under tension by a fishing line that spanned from the top of the fishing rod to a lifting solenoid. When the solenoid was activated, the fishing rod flicked upwards and the mealworm was instantaneously removed. The behavior of bats attacking the mealworm was recorded with a T-shaped four-microphone array. The distance between adjacent microphones (Mic) was 1.5 m. Two high-speed video cameras (Cam) and two infrared lights (IR) were mounted on the T-shaped framework such that the optical axes of the video cameras (dashes lines) were perpendicular to each other. The mealworm was positioned close to the interception point of the optical axes of the cameras about 1.5 m in front of the T-shaped framework.

We recorded *M. daubentonii* attacking the mealworm with a T-shaped four-microphone array with three ultrasonic microphones (Sanken CO100K, Tokyo, Japan) arranged horizontally at intervals of 1.5 m and one 1.5 m above the centre microphone. Two high-speed video cameras (Basler A600f, Basler AG, Ahrensburg, Germany) were also mounted on this T-shaped framework with a separation of 2.9 m and their optical axes perpendicular to each other. An infrared light (IR-Strahler MEGA-LED XL, ABUS, Wetter-Volmarstein, Germany) was attached next to each camera (fig. 3.1). The mealworm was positioned about 1.5 m in front of the T-shaped framework close to the interception point of the optical axes of the cameras.

3.3.1.3 Experimental procedure

Data acquisition was controlled by laptop 1 running MATLAB 7.5 (Mathworks, Natick, MA) with the professional MATLAB audio tool SoundMexPro (HörTech gGmbH, Oldenburg, Germany). When the experimental trials were running, a trigger signal was sent to the cameras every 10.2 ms via an audio interface (Motu Traveler, Motu, Cambridge, UK) to ensure a synchronized video acquisition with a frame rate of 98 Hz.

Information from the cameras was sent to laptop 2 running a customized program version of EyeSeeCam (Schneider *et al*. 2009) in which the eye-tracking module was replaced by a dedicated bat-tracking module programmed for this experiment by Thomas Dera. The program determined the position of the bat and calculated the distance between the center of the bat and the mealworm for each frame (i.e. every 10.2 ms). When the distance between the bat and the mealworm dropped below a predefined threshold value, the program initiated the activation of the solenoid and the mealworm was removed. During a trial, the video information was stored in a 5 s ring buffer. When the trial was stopped by the experimenter, the last 490 frames of each camera were saved to hard disk for further analyses.

During a trial, the signals recorded by the four microphones were A/D converted at 192 kHz by the audio interface and sent to laptop 1. The digitized audio signals, the video trigger signal and the electrical signal leading to the activation of the solenoid were stored in a 5 s ring buffer that was saved to hard disk at the end of each trial. Audio data acquisition and emission of camera trigger signals were stopped simultaneously at the end of each trial to ensure that the audio and video recordings were synchronized.

At first we recorded the bats attacking the prey without removing the mealworm. These controls were used to describe and quantify the typical hunting behavior of *M. daubentonii* during aerial captures. When the bats were accustomed to the setup we ran trials with and without prey removal in a random order. The distances between the bat and the mealworm at the time of prey removal were varied between about 2-80 cm corresponding to about 6-240 ms before expected time of contact. The time from prey removal to expected contact was determined from the video recordings for each trial. 28 controls and 126 removal trials were recorded at the first recording site and 75 controls and 124 removal trials at the second recording site.

3.3.2 Trawling captures in the laboratory

3.3.2.1 Bats

Three *M. daubentonii* were caught in a mist net over a river (Odense Å) in Odense, Denmark and trained to catch mealworms placed on the surface of an indoor pond (2.5 x 1 m, water level 15 cm) inside a flight room (7 × 4.8 × 2.5 m). During the experimental period the bats were only fed during experiments, but they had continuous access to drinking water.

3.3.2.2 Experimental setup

During experimental trials all capture sequences were recorded with a trigger-synchronized setup with high-speed video and a T-shaped array of four microphones for sound recordings. The trigger also activated the custom built prey remover device used to pull the mealworm below the water surface (fig. 3.2). A Mikrotron highspeed camera (EoSens MC1362, Mikrotron GmbH, Unterschleissheim, Germany) and frame grabber card (Mikrotron Inspecta-5 PCI-X) installed on an HP PC were used to record video sequences at a frame rate of 300 Hz. Sequences were stored onto a ring buffer and after triggering, recordings were saved on the PC with 1.5 s pre-trigger time (450 frames) and 1 s post-trigger time (300 frames) giving a total duration of each video file of 2.5 s (750 frames). Three infrared lights (λ 850 nm, model 995JH, Kinapriser.dk) were used to illuminate the area of the pool surrounding the mealworm.

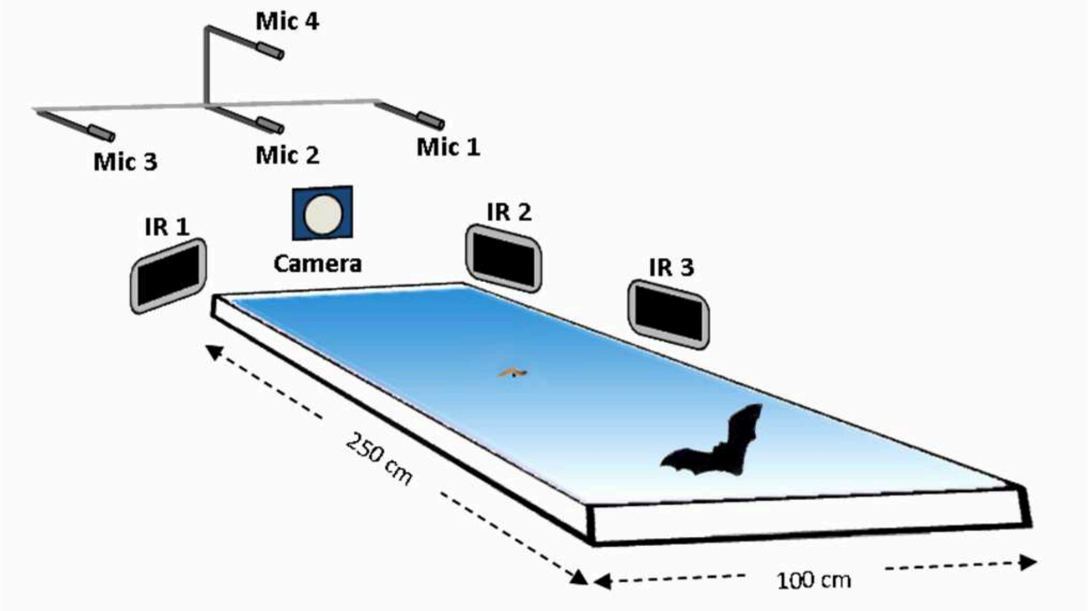

Figure 3.2: Laboratory setup
The figure shows a schematic of the laboratory setup. Mealworms were attached to a custom built prey remover device on the surface of an artificial pond. The mealworm could be removed by pulling it under the water surface. The echolocation behavior of bats attacking the mealworm was recorded with a T-shaped four-microphone array. The distance between the three horizontal microphones (Mic) was 40 cm and the fourth microphone was placed 35 cm above microphone 2. A high-speed video camera and three infrared lights (IR) were used to record video sequences.

Echolocation calls were recorded with four G.R.A.S. ¼" condenser microphones (40 BF, G.R.A.S. Sound and Vibration A/S, Holte, Denmark), three spaced 40 cm apart on a horizontal axis and the fourth displaced 35 cm above the center horizontal axis microphone. Signals were pre-amplified (G.R.A.S. 26AC), amplified (G.R.A.S. AA, +40 dB, built-in 15 kHz high pass filters) and sampled at a rate of 300 kHz/channel by an Avisoft UltraSoundGate A/D converter (1216H, Avisoft Bioacoustics, Berlin, Germany). Sound recordings were stored on a Lenovo X60 laptop (Lenovo Danmark ApS, Holte, Denmark). The custom built prey remover device consisted of an Arduino board controlling a small electromotor connected via carbon fishing line (Ø 0.25 mm) to a spring inside the actual "remover", a hollow plastic cylinder with a small metal needle tip attached to the top. Upon triggering the electromotor pulled on the cylinder via the fishing line, causing it to slide down into a bigger cylinder firmly anchored under water, thus moving the metal tip with the worm below the surface, out of the bats' trajectory. Triggering was done manually when the bat approached the worm. For audio-video synchronization, a green diode was turned on within the view of the high speed camera at the time of triggering and, simultaneously, a 5 V signal from a custom-built trigger unit was recorded on a fifth channel of the A/D converter.

3.3.2.3 Experimental trials

During experimental trials, a single bat was allowed to fly freely in the flight room while presented with sets of three different trial types in a randomized order (http://www.randomizer.org/). We included two different types of control trials. In one type, surface controls, the tip of the prey remover was pulled under water before beginning of the trial and anchored there for the duration of the trial. A mealworm was then placed on the water surface above the position of the remover device but floating freely. In the second type of controls, worm-on-device, a mealworm was attached to the metal tip of the prey remover by piercing it from below just as in actual removal trials, but the prey remover motor was unplugged, so the worm did not move when the setup was triggered. In the experimental removal trials a mealworm was placed on the prey remover and the motor was activated by triggering, thereby pulling the worm below the water surface.

The delay from triggering until the worm was pulled below the water surface by the electromotor was not completely constant due to the properties of the fishing line, but was measured for each trial from the high speed video showing both the synchronization diode signal and disappearance of the mealworm. Trials were presented in subsets of 12. The position of the prey remover in the pond was changed before each subset and camera focus and infrared lighting adjusted accordingly. Up to 4 subsets (48 single trials) could be run continuously before the bats were not hungry anymore and lost motivation which they showed by landing on the ceiling of the flight room and staying there. The mealworm was removed at arbitrary times between 3 and 240 ms before expected times of contact, as was estimated from the number of video frames from removal to when the bat was directly above the position of the worm before it was pulled under. We recorded 217 surface controls, 219 worm-on-device controls and 128 removal trials.

3.3.3 Startle response reaction times

To obtain an estimate of minimum reaction times we measured the startle response in the three *M. daubentonii* from the laboratory experiments using an intense sound source (a clicker) and high speed video. Each bat was wrapped gently in cloth with the head free and fixed in a stationary position by attaching the cloth to a clamp. We used the same high speed video camera and triggering system as in the removal trials, with one channel of the A/D converter recording the clicker sound and another the short-circuiting pulse from the trigger, synchronized to the illumination of the green diode within the video frame. In addition, the experimenter’s hand sounding the clicker was recorded inside the video frame. We timed the delay from onset of the clicker sound until the bats' ear pinnae flicked and cross checked the synchronization by counting the number of video frames from clicker activation (clearly visible on the video as motion blur along the edge of the clicker buckle) to flicking of the pinnae.

3.3.4 Data analysis

High speed video and sound recordings from the field and laboratory were analyzed to determine the reaction to prey removal at different times relative to expected prey capture. We analyzed temporal acoustic features of the echolocation calls (call timing, call intervals, number of calls in the different echolocation phases) as well as the capture related flight behavior. To simplify matters, this capture related flight behavior is referred to as capture behavior throughout this thesis. We subdivided the capture behavior into four stages: lowering of the hind legs, moving the head towards the tail membrane, curling up completely and uncurling to continue flight.

Sound recordings from the field were analyzed using MATLAB v. 7.5 and BatSound Pro 3.1. Call times and pulse intervals (PIs, i.e. time between the start of consecutive calls) were extracted by manually clicking on the calls in a spectrogram (Hamming window, FFT size: 256, overlap: 98%). Sound recordings from the flight room experiments were analyzed in MATLAB 7.7 with a custom written script, which detected each call and extracted call times and pulse intervals. Extracted values were then cross-checked manually in Batsound Pro 4.0 to exclude any errors. The first buzz 1 call was defined as the call following the last PI longer than 15 ms. Buzz 2 was characterized by PIs shorter than 6.5 ms.

Videos from the field were brightened and converted into multi-image tif-files. For each behavioral category we counted the number of frames in which the bat performed the corresponding behavior to determine the duration of the phase. In field trials with prey removal the release of the fishing rod produced a characteristic sound which appeared in the sound recordings. By comparing the onset of this sound with the number of the frame where the mealworm first started to move upwards, the audio-video synchronization was verified.

Highspeed video recordings from the flight room were analyzed using MotionBlitz software (MotionBlitz Director v. 3.04.0003 and MotionBlitz Cube v. 1.11.28, Mikrotron GmbH, Unterschleissheim, Germany). As for the field data, we calculated the timing and duration of each behavioral stage by counting the number of frames in the high speed video.

Reaction times were determined by calculating the time between prey removal and the abortion of the bat's echolocation or capture behavior. Only trials with prey removal times at which the bat’s echolocation or capture behavior deviated significantly from the control behavior were included in the reaction time analysis.

3.3.5 Statistical tests

Statistical analyses were done with the Statistics Toolbox for MATLAB 7.5. We show medians (first quartile - third quartile) and used nonparametric tests (Mann-Whitney U-test and Kruskal-Wallis for multiple comparison followed by Tukey's HSD (honestly significant difference criterion) post hoc tests). A significance level of $p<0.05$ was assumed for all analyses. We tested whether the bats changed their echolocation and capture behavior when the prey was removed at different times before prey capture compared to the controls where prey was not removed. To do this, we subdivided trials with prey removal times between 0 ms and 240 ms before contact into eight groups with a bin size of 30 ms. The number of buzz 2 calls and duration of capture behavior of the different groups were tested against that of the corresponding control groups.

3.4 Results

3.4.1 Insect captures in air and over water

In the field, wild *M. daubentonii* learned to capture a tethered mealworm presented about 40 cm above a water surface. The bats caught the prey by lowering their hind legs, catching the mealworm in the tail membrane and moving their head towards the tail membrane to curl up into a complete ball shape while transferring the mealworm to the mouth. The median capture behavior from lowering the hind legs until starting to uncurl lasted 296 ms (224-367 ms). Lowering of the hind legs lasted 41 ms (41-51 ms), moving the head towards the tail membrane lasted 20 ms (20-31 ms) and being curled up completely lasted 235 ms (153-306 ms). The typical echolocation behavior in these aerial captures consisted of an approach phase and a terminal buzz; the latter clearly separable into buzz 1 and buzz 2. The bats emitted a median of 11 (10-13) buzz 1 and 19 (18-21) buzz 2 calls. Buzz 1 started about 200 ms and buzz 2 about 110 ms before prey contact. Capture and vocalization behavior is illustrated in figure 3.3 A and quantified in figures 3.4 and 3.7 (top half).

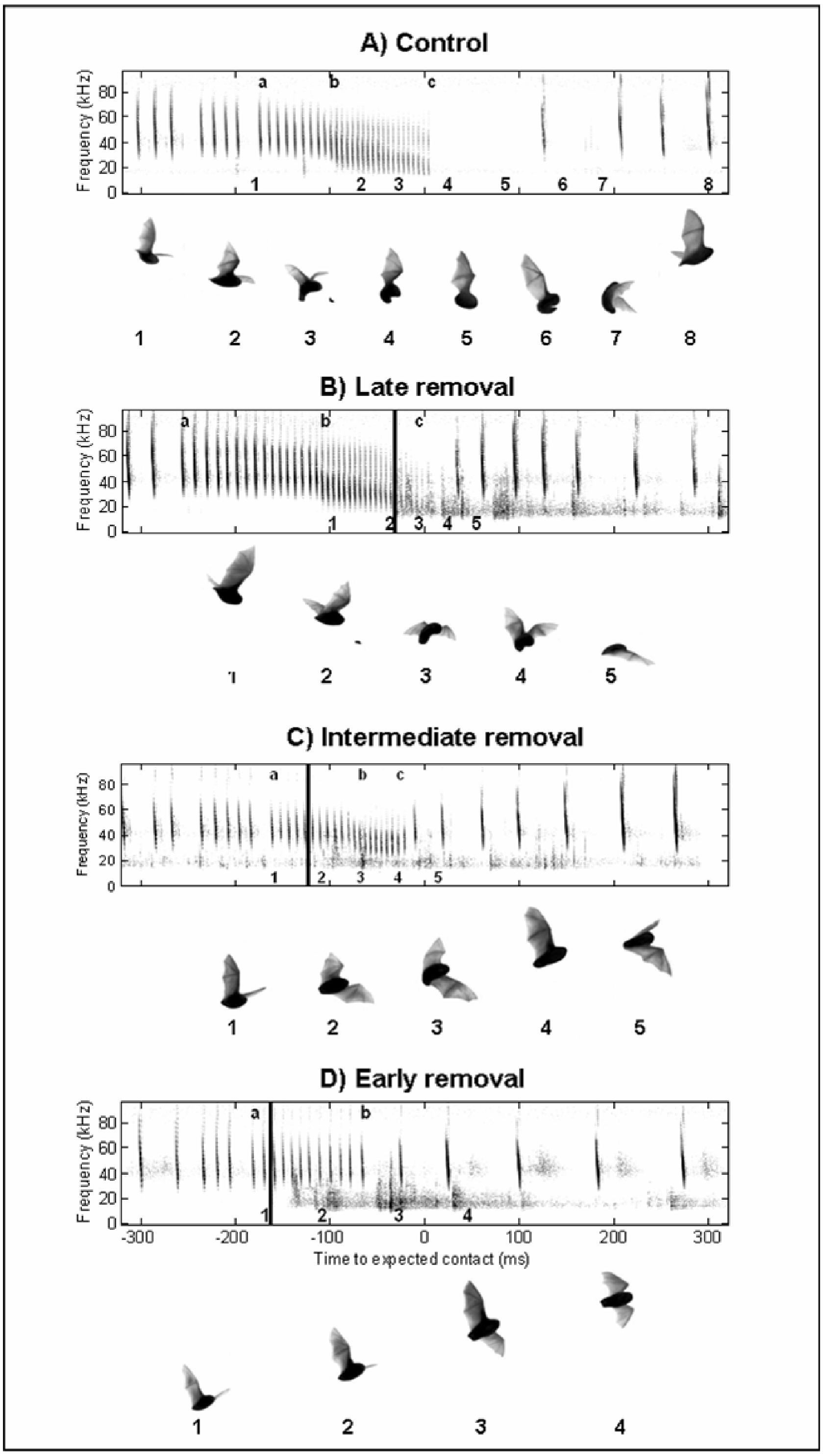

Figure 3.3 Examples of aerial captures in the field
The four panels illustrate examples of *Myotis daubentonii*'s acoustic behavior (spectrograms) and capture behavior (bat silhouettes derived from video snapshots) during prey capture sequences recorded in the field experiment. A) control trial of the bat catching a mealworm, followed by three prey removal sequences where the mealworm was removed B) late, C) intermediate and D) early in the sequence relative to expected contact. Numbers in the spectrograms correspond to the numbers in each of the snapshots below. Letters in the spectrograms denote the different phases of the echolocation sequence (a: start of buzz 1, b: start of buzz 2/end of buzz 1, c: end of buzz 2). The black vertical line indicates the time of prey removal. The earlier the prey is removed, the shorter the capture behavior and buzz 2 sequence compared to the control. At the early removal example (panel D) the bat does not emit a buzz 2 and no capture behavior is initiated.

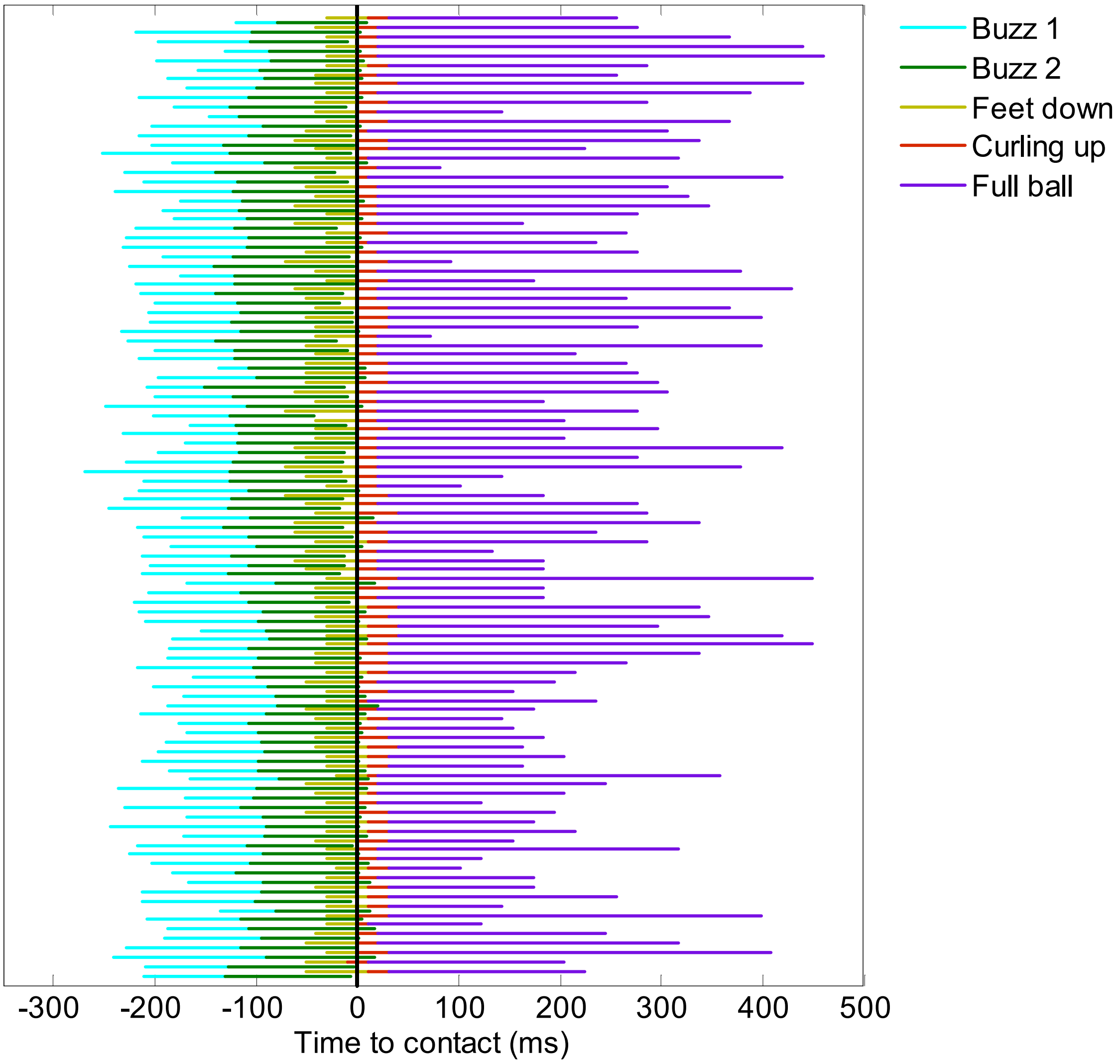

Figure 3.4 Relative timing of echolocation and capture behavior in the control trials for aerial captures in the field
The graph shows the timing of buzz 1 (cyan), buzz 2 (green) and the different phases of prey capture behavior (feet down: yellow, curling up: red and full ball: purple) relative to bat-prey contact for each individual control trial.

In the flight room, three *M. daubentonii* were trained to capture a mealworm presented directly on the water surface, either floating freely or pinned to the prey remover device. Again, the bats caught the prey by lowering their hind legs, but in contrast to aerial captures they caught the mealworm with their feet and moved the feet to the mouth. The echolocation behavior was qualitatively similar to the aerial captures in the field, but both buzz 1 and buzz 2 were shorter. There were small, but significant ($p<0.001$, Mann-Whitney U-test) differences between the surface and the worm-on-device controls. The capture behavior from lowering the feet until start of uncurling lasted 157 ms (145-185 ms) in the surface controls and 177 ms (150-212 ms) in worm-on-device controls. Lowering of the hind legs lasted 63 ms (57-73 ms) and 67 ms (57-77 ms), moving the head towards the tail membrane lasted 47 ms (43-57 ms) and 50 ms (43-60 ms) and being curled up completely lasted 43 ms (33-57 ms) and 52 ms (37-93 ms) for surface and worm-on-device controls, respectively. In both types of controls, the buzz 1 phase started around 130 ms before time of capture and lasted ca. 55 ms. The bats emitted a median of 5 (4-6) buzz 1 calls in surface controls and 6 (5-6) buzz 1 calls in worm-on-device controls. The buzz 2 phase started ca. 80 ms before time of contact with median number of buzz 2 calls of 11 (10-12) in surface and 11 (10-14) in worm-on-device controls. In the following we focus on the worm-on-device controls as those are more similar to the removal trials. The trawling capture behavior is exemplified in figure 3.5 and the trawling as well as the vocalization behavior in the worm-on-device controls are quantified in figures 3.6 and 3.7 (bottom half).

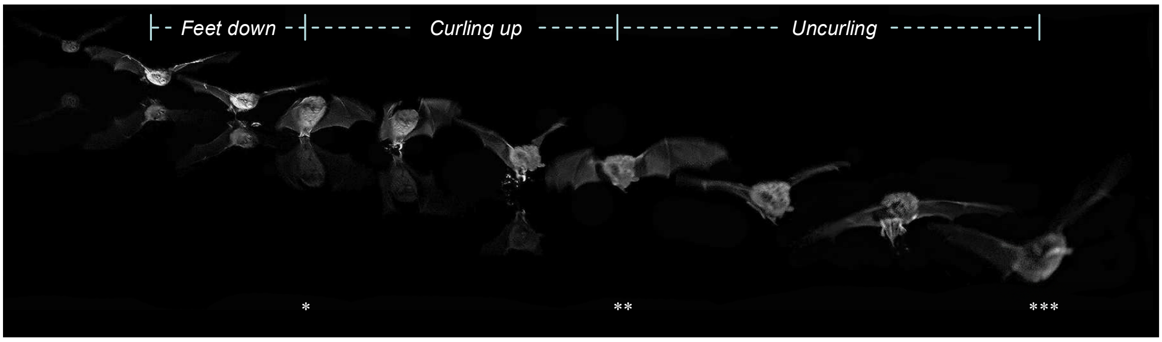

Figure 3.5: Illustration of the different stages of capture behavior during trawling
The figure depicts a series of snapshots of a Daubenton’s bat trawling a mealworm from the water surface. The bats caught the prey by lowering their hind legs, catching the mealworm with their feet and moving the feet to the mouth. The capture behavior can be subdivided into the phases “feet down”, “curling up”, “full ball” and uncurling. * bat-prey contact, ** the bat is curled up completely and forms a full ball, *** the bat has uncurled completely and resumes its search flight

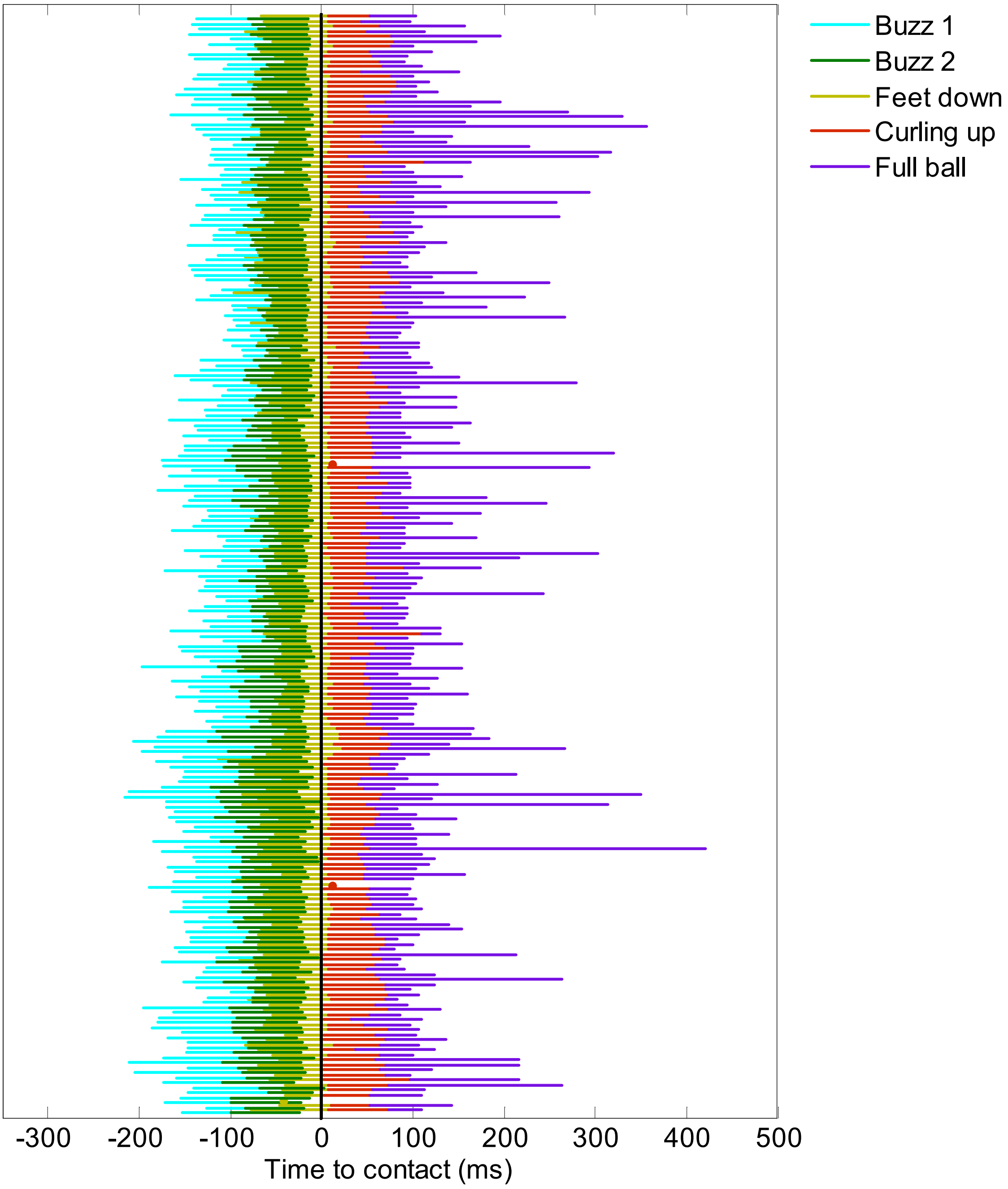

Figure 3.6 Relative timing of echolocation and capture behavior in the control trials for trawling captures in the laboratory with the worm fastened to the remover device The graphs show the timing of buzz 1 (cyan), buzz 2 (green) and the different phases of prey capture behavior (feet down: yellow, curling up: red and full ball: purple) relative to bat-prey contact for each individual control trial.

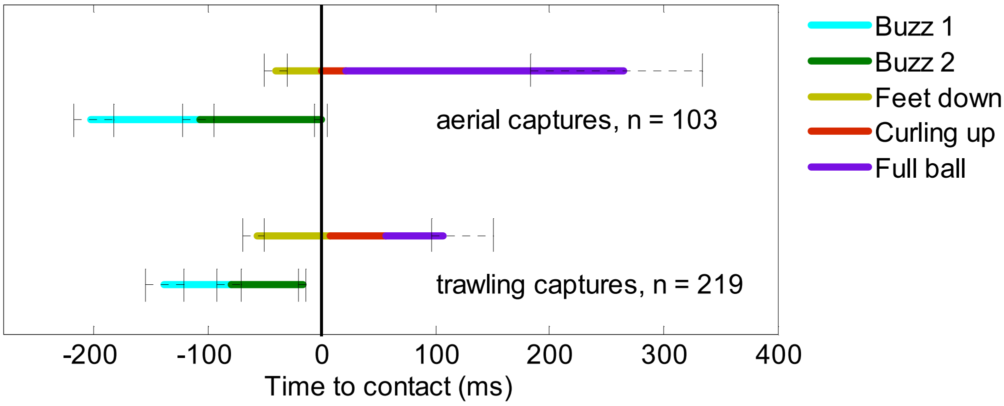

Figure 3.7 Relative timing of echolocation and capture behavior in the controls: summary figure

The graphs depict the median as well as the first and third quartile of the start and stop times of buzz 1 (cyan), buzz 2 (green) and the prey capture behavior (yellow, red and purple) relative to bat-prey contact. The different colors of the capture behavior denote the durations of the different capture phases (feet down: yellow, curling up: red and full ball: purple). The number of control trials (n) is given in each graph. Top: control trials for aerial captures in the field, Bottom: control trials for trawling captures in the laboratory with the worm fastened to the remover device.

3.4.2 Prey removal

In the field, the mealworm was tethered to a fishing line suspended from a fishing rod, and we removed it by releasing the anchoring line of the fishing rod such that it flicked upwards and removed the prey instantaneously. When prey was removed late (< 90 ms) before expected contact, the bats showed the same echolocation behavior as in controls without prey removal. When prey was removed earlier than 90 ms before expected contact, the bats emitted significantly fewer buzz 2 calls (Kruskal-Wallis and multiple comparison test, $p<0.05$, fig. 3.8 A). Importantly, buzz 2 was not an all-or-nothing event, rather, it was gradually shortened, i.e. the earlier prey was removed the fewer buzz 2 calls were emitted. Buzz 2 was completely omitted in 71% of all trials when the prey was removed more than 150 ms before expected contact. Complete omission of buzz 2 was observed in trials with prey removal times down to 112 ms before expected contact (figs. 3.8 A, 3.9 and 3.10).

Whereas vocal echolocation behavior in prey removal trials in air was indistinguishable from controls when prey was removed later than 90 ms before expected contact, the sequence of maneuvers involved in seizing the prey, the capture behavior, was always significantly shorter in trials with prey removal than in the controls (Kruskal-Wallis and multiple comparison test, $p<0.05$, fig. 3.8 C). When prey was removed earlier than 150 ms before expected contact, no capture behavior was initiated in 53% of all trials. In some cases we observed a complete lack of capture behavior at prey removal times as late as 60 ms before contact (figs. 3.8 C, 3.9 and 3.10). The reduced duration of capture behavior in removal trials was mainly due to the fact that in contrast to controls the bats rarely curled up completely even when prey was removed immediately before expected contact. At early prey removal times the capture behavior merely consisted of lowering the hind legs or was not initiated at all (figs. 3.3 B-D, 3.9, and 3.10).

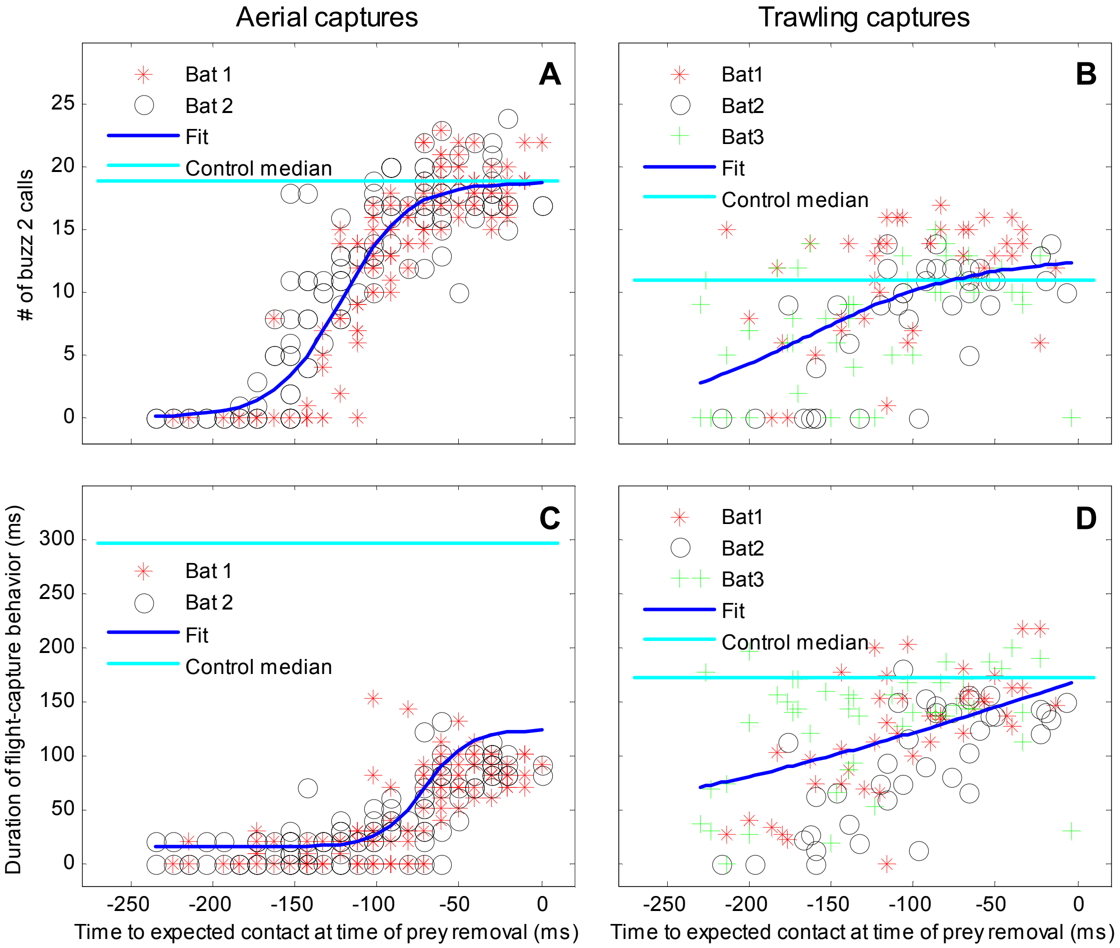

Figure 3.8: Number of buzz 2 calls and duration of flight capture behavior
The graphs depict the number of buzz 2 calls (top) and the duration of the capture behavior (bottom) of the removal trials as a function of the time of prey removal for aerial captures in the field (left) and trawling captures in the laboratory (right). Different symbols and colors are used for different bats. A sigmoid function has been fitted to the whole data sets (all bats, blue line). For comparison, the median number of buzz 2 calls and the median duration of capture behavior of the controls for aerial captures in the field (left) and of the worm-on-device controls for trawling captures in the laboratory (right) are illustrated as cyan horizontal line.

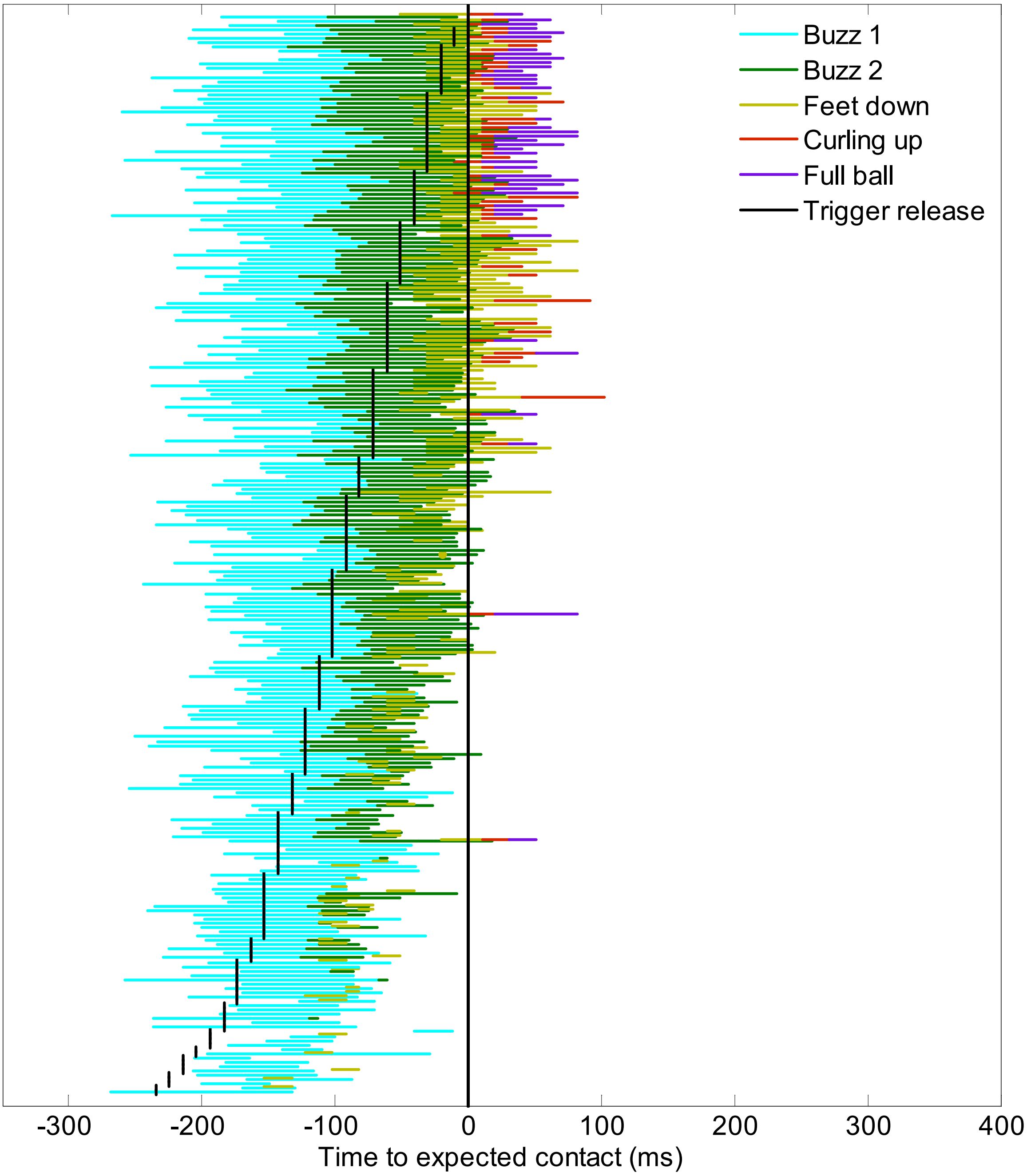

Figure 3.9: Relative timing of echolocation and capture behavior in prey removal trials for aerial captures in the field

The graphs show the timing of buzz 1 (cyan), buzz 2 (green) and the different phases of prey capture behavior (feet down: yellow, curling up: red and full ball: purple) relative to expected bat-prey contact for each individual removal trial. The black vertical lines denote the time of prey removal.

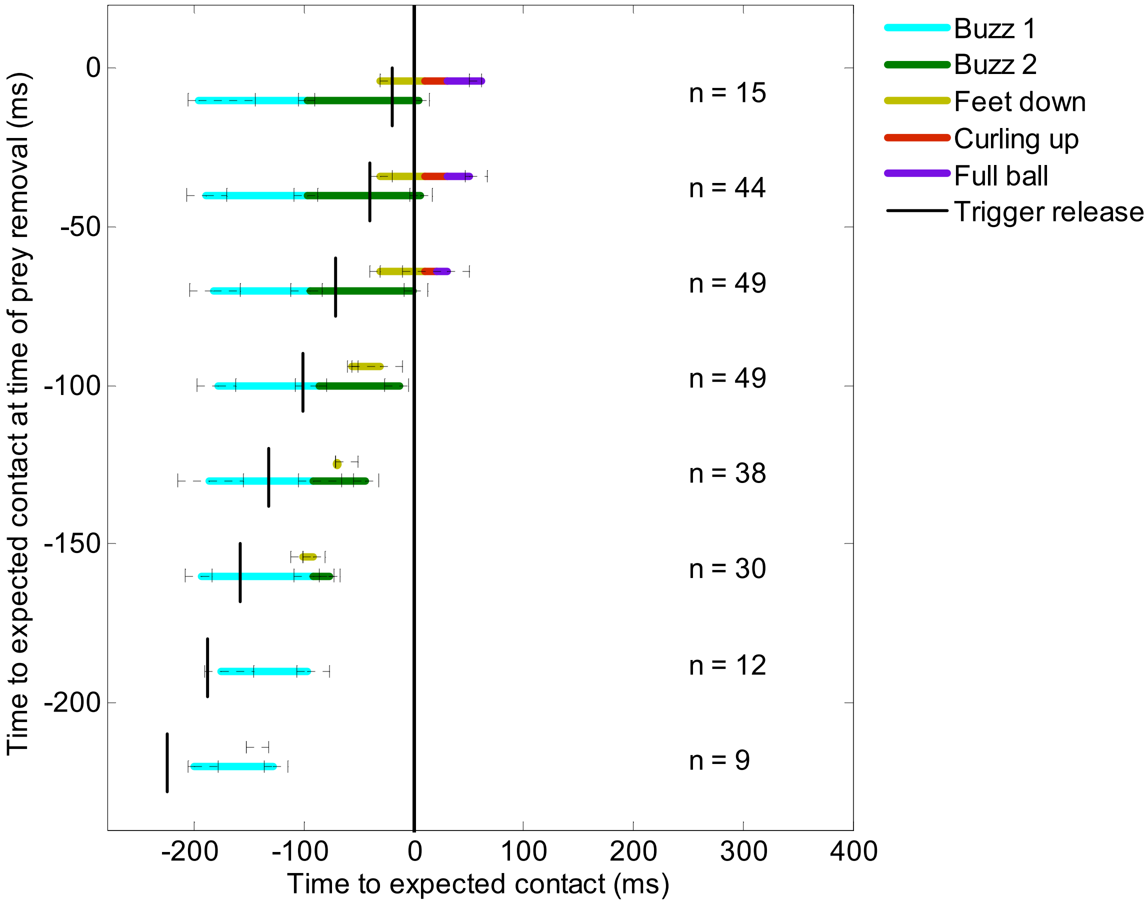

Figure 3.10: Relative timing of echolocation and capture behavior in prey removal trials for aerial captures in the field: summary figure

The trials with prey removal times between 0 and 240 ms before contact were divided into eight groups with a bin size of 30 ms. The relative timing of echolocation and capture behavior is depicted for each group at different positions on the y-axis. The number of trials (n) in each group is given in the figure. The graphs depict the median as well as the first and third quartile of the start and stop times of buzz 1 (cyan), buzz 2 (green) and the prey capture behavior (yellow, red and purple) relative to expected bat-prey contact. The different colors of the capture behavior denote the durations of the different capture phases (feet down: yellow, curling up: red and full ball: purple). The black vertical lines denote the time of prey removal.

In the flight room, where the bats were trawling for mealworms on the water surface, the prey was removed by pulling it beneath the water surface. As with aerial captures in the field, late prey removals resulted in echolocation behavior similar to the controls. The limit for eliciting the complete echolocation behavior in flight room experiments was 120 ms for all three bats (Kruskal-Wallis and multiple comparison test, $p<0.05$, fig. 3.8 B).

When the prey was removed earlier than 120 ms before expected contact, the bats emitted significantly fewer buzz 2 calls than in the controls (Kruskal-Wallis and multiple comparison test, $p<0.05$, fig. 3.8 B). As in the field experiments, the duration of buzz 2 decreased gradually the earlier the prey was removed. Buzz 2 was completely omitted in 38% of all trials when the prey was removed earlier than 150 ms before expected contact and in some trials down to prey removal times as late as 97 ms before contact (figs. 3.8 B, 3.11 and 3.12). In contrast to aerial captures, the duration of capture behavior in trawling captures was indistinguishable from controls if the prey was removed late (< 60 ms before contact, Fig. 3.8 D). When the prey was removed earlier than 60 ms before expected contact, the bats significantly shortened the capture behavior (Kruskal-Wallis and multiple comparison test, $p<0.05$). However, even when the prey was removed earlier than 150 ms before expected contact, capture behavior was initiated in 88% of all trials (figs. 3.8 D, 3.11 and 3.12).

In both, aerial and trawling captures, the duration of the echolocation and capture behavior decreased with increasing time between prey removal and expected contact time. However, the correlation between the time of prey removal (relative to expected contact) and the duration of the echolocation and capture behavior is stronger in aerial captures than in trawling captures as the bats in the trawling captures showed an (almost) complete terminal buzz and capture behavior in a number of trials even though the prey was removed quite early (fig. 3.11).

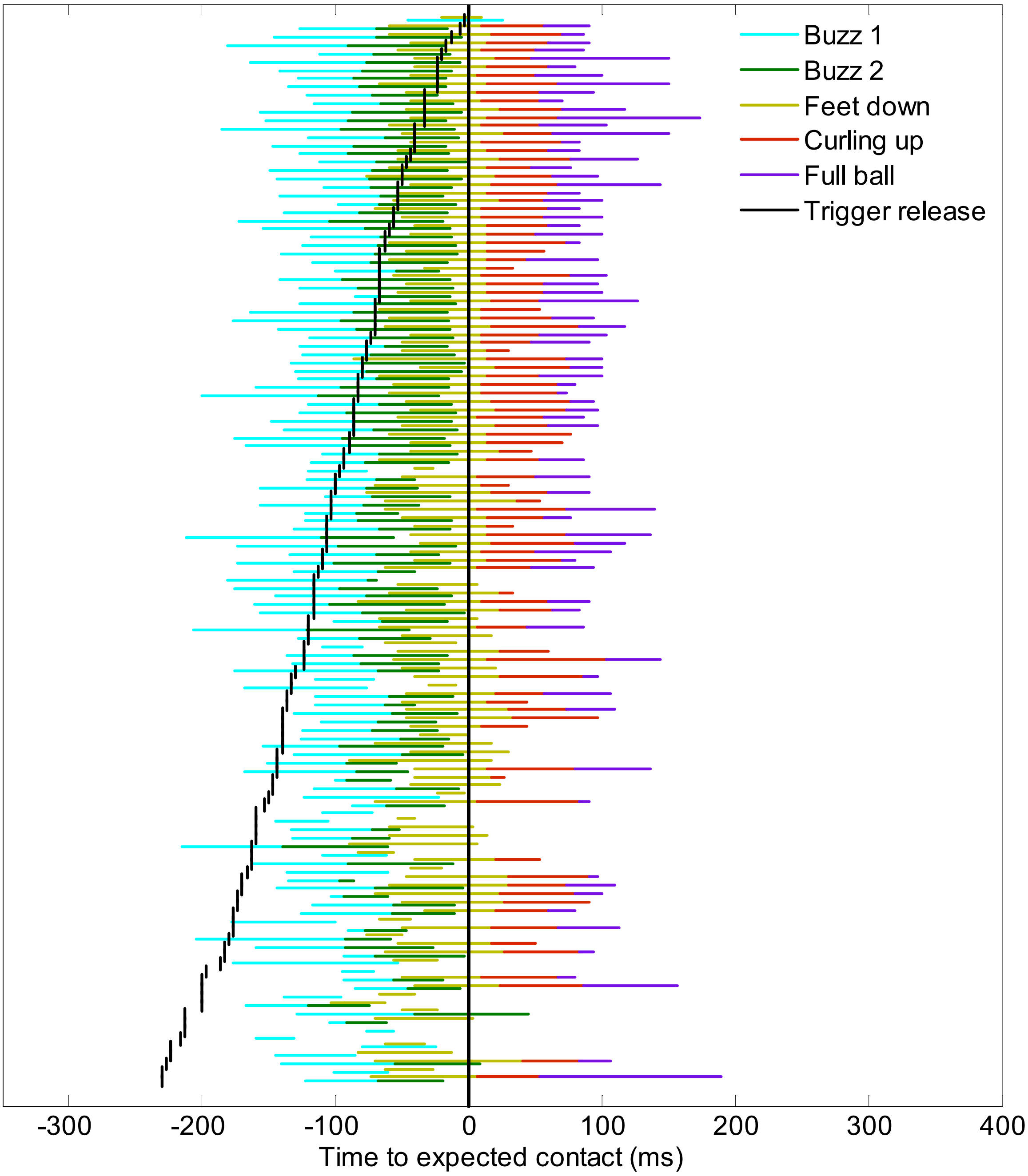

Figure 3.11: Relative timing of echolocation and capture behavior in prey removal trials for trawling captures in the laboratory
The graphs show the timing of buzz 1 (cyan), buzz 2 (green) and the different phases of prey capture behavior (feet down: yellow, curling up: red and full ball: purple) relative to expected bat-prey contact for each individual removal trial. The black vertical lines denote the time of prey removal.

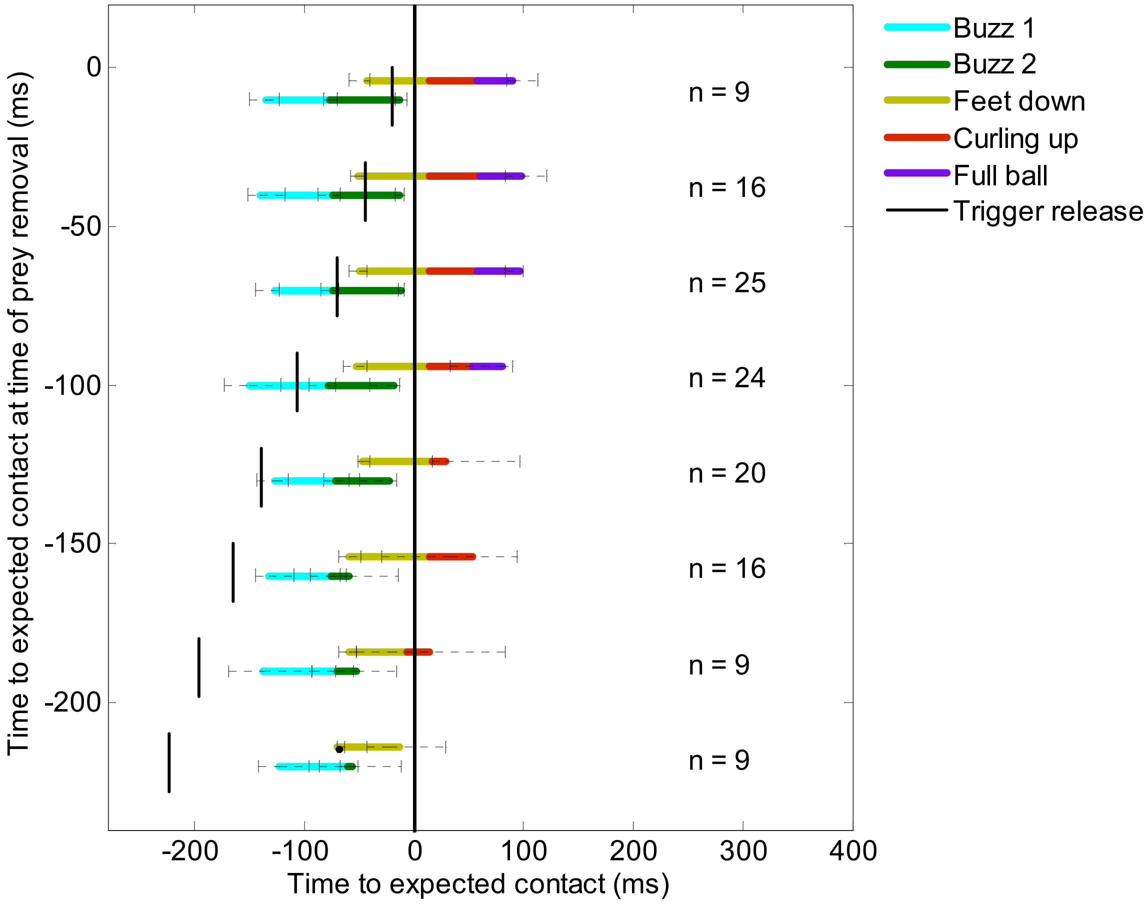

Figure 3.12: Relative timing of echolocation and capture behavior in prey removal trials for trawling captures in the laboratory: summary figure

The trials with prey removal times between 0 and 240 ms before contact were divided into eight groups with a bin size of 30 ms. The relative timing of echolocation and capture behavior is depicted for each group at different positions on the y-axis. The number of trials (n) in each group is given in the figure. The graphs depict the median as well as the first and third quartile of the start and stop times of buzz 1 (cyan), buzz 2 (green) and the prey capture behavior (yellow, red and purple) relative to expected bat-prey contact. The different colors of the capture behavior denote the durations of the different capture phases (feet down: yellow, curling up: red and full ball: purple). The black vertical lines denote the time of prey removal.

3.4.3 Reaction times

From the prey removal experiments we estimated reaction time by calculating the time between removal of the mealworm and the first behavioral or acoustic deviation from the controls. The acoustic reaction time, measured as the median delay from prey removal to adjustment of echolocation behavior, i.e. abortion of the terminal buzz, was 87 ms (76-101 ms, n = 138) in aerial captures and 123 ms (100-152 ms, n = 54) in trawling captures. The behavioral reaction time, measured as the median delay from prey removal to abortion of the capture behavior, was 82 ms (71-102 ms, n = 183) for aerial captures and 178 ms (150-217 ms, n = 98) for captures from the water surface. Median reaction times were 36 to 96 ms longer in trawling captures than in aerial captures.

Finally, we quantified absolute minimum reaction times in *M. daubentonii* for passive acoustic input in terms of an acoustic startle response (ear movements) to a loud sound from a hand-held clicker. The median delay from onset of the clicker sound to the beginning of ear movement was 29 ms (19-41 ms), 19 ms (17-28 ms) and 18 ms (16-21 ms) for the same three individuals trained to perform the flight room prey removal experiments.

3.5 Discussion

The current study presents a unique dataset where we interrupt the auditory and somatosensory feedback to a sonar-guided predator during the terminal phase of prey pursuit. The results clearly demonstrate that motor control of vocal and capture behavior are not fixed patterns, but subject to fast and flexible adaptations in response to changes in the perceptual stream of data from the prey object even at the last phases of prey capture.

Even for hunting bats in the terminal buzz, echolocation is coupled to auditory feedback information from returning echoes. Specifically, the duration of buzz 2 is gradually decreased depending on the time within buzz 1 when the bat receives the echo-acoustic information that the prey has been removed. These data indicate a sonar reaction time (as seen in a change of vocalization behavior) of 87 and 123 ms in aerial and trawling captures, respectively. Interestingly, the capture behavior was quite different in aerial vs. trawling trials: in trawling trials, late removals resulted in the full capture behavior, whereas in aerial trials, the capture behavior was always dramatically shortened even when the prey was removed very close to expected contact. This might indicate that somatosensory information also plays an important role in prey capture. Based on changes of capture behavior, the data revealed a reaction time of 82 and 178 ms in aerial and trawling trials, respectively.

3.5.1 Echolocation behavior

There were small but significant differences between echolocation behavior in the aerial captures and trawling captures. In aerial captures, bats emitted more calls in buzz 1 and buzz 2, both of which also had longer overall durations and were initiated earlier relative to expected prey contact than in trawling captures (fig. 3.7). This difference might relate to the fact that localization of prey in air requires 3D-positioning, whereas the possible positions of prey on the water surface only varies in two dimensions. Both aerial and trawling captures are part of *M. daubentonii’*s natural repertoire, although trawling is by far the dominant hunting strategy (Kalko & Schnitzler 1989).

3.5.2 Capture behavior

In contrast to the echolocation behavior, there were substantial differences between capture behavior in air and over water (Figs. 3.7). In the wild the behavioral stages in both types of captures are the same and duration of the capture behavior ranges from 150-200 ms (Kalko & Schnitzler 1989). We found similar median durations of capture behavior, 177 ms, in the worm-on-device controls in trawling captures, but aerial captures lasted much longer with a median duration of 296 ms. While the feet down and curling up phases are slightly shorter, the full ball phase is much longer in aerial than in trawling captures. This indicates that it is more difficult for the bats to retrieve the mealworm in aerial captures, in which the mealworm is stored in the pouch, than in trawling captures, in which the mealworm is grabbed with the feet. The difference could also be introduced by the artificial situation in the field where the mealworm was tethered to a thin line, potentially complicating prey seizing by the bats. Despite the possible artificial situation, this is an important result as it underlines the flexibility in motor control of the capture behavior. The bats may also sometimes prolong the head-down stage in the field, probably due to difficulties in retrieving the prey from the pouch (Kalko & Schnitzler 1989).

3.5.3 Prey removal

In air as well as over water the bats changed their echolocation behavior compared to controls when prey was removed earlier than about 100 ms before expected contact. 100 ms time to expected contact corresponds to a distance of ca. 33 cm between bat and prey. At this distance to the prey the delay between each emitted call and the returning echo is only about 2 ms. Therefore, the bat’s reaction time is largely equal to the delay between trigger-release and acoustic reaction, i.e. 87 and 123 ms in aerial and trawling trials, respectively. The median behavioral reaction time is much longer in trawling captures (178 ms) than in aerial captures (82 ms). The larger variation in trawling captures (figs. 3.9 - 3.12) may partly be due to the fact that the bats sometimes seemed to trawl with their feet through the water even though the prey had been removed early. We hypothesize that the animals resign to this strategy because, as it is true in the wild, the removed prey may still be present just below the surface and still accessible with the bat's large hind feet although it is not detectable with echolocation anymore.

The reported reaction times on the order of 100 ms are in agreement with earlier estimates from pulse intervals or behavioral studies (Masters *et al*. 1985; Ghose *et al*. 2006; Melcon *et al*. 2007), but much longer than our estimates based on the startle response (ca. 20 ms). The startle response represents a lower limit for the time required from sensory input to a simple motor output (here; flicking of the bats' ears) and may only be relevant for reflex-like behavior. Here we found fairly constant delays from acoustic feedback to reaction for different removal times, indicating that the bat needs a processing time of approximately 100 ms for analyzing the auditory feedback and reacting with a motor response.

When disrupting the acoustic feedback by removing the prey later than about 60 ms before contact, the capture behavior over water was similar to controls. Yet, no matter how late the prey was removed, capture behavior in air was always much shorter than in controls. This result might reflect the fact that the bats had to remove the mealworm from the fishing line, and thus, the phase during which the bats were rolled up in a full ball is likely to be unnaturally extended in the controls rather than unnaturally short in the trials where the prey was removed. However, the result may also point to the importance of multimodal sensing through both hearing and somatosensory feedback because in aerial captures the bats receive no mechanoreceptor feedback from the tail membrane, if prey is removed. In contrast, trawling bats lower the feet and tail to touch the water, and thus get sensory input to mechanoreceptors even if the prey is removed. We saw several instances of the bats in the trawling trials curling up once with the head in the pouch, uncurling partly and then curling up a second time as if puzzled and searching again for the prey they thought they had grasped. Somatosensory feedback has not been studied much in bats, but new evidence underlines that hunting and flight behavior in bats is adapted to multi-sensory feedback (Sterbing-D'Angelo *et al*. 2011).

3.5.4 General findings

We have presented a series of results with implications for our general understanding of active motor control in response to perceptual feedback through sensory information. The results suggest minimum reaction times of around 100 ms which is within the range indicated by earlier experiments with echolocation. The high repetition rate in the buzz, up to 180-200 Hz in buzz 2, would fuse to a continuous input if perception were visual, but the auditory system might be fast enough to parse this into a series of snapshots. Our data demonstrate a gradual decrease of buzz 2 duration. Other field data show buzz 2 durations ranging from 38 to 69 ms (Kalko & Schnitzler 1989) or as much as 40 to 200 ms in *Pipistrellus kuhli* (Schnitzler et al. 1987). These variations in buzz duration highlight the tight sensory-motor coupling of echolocation even during the terminal buzz. The current data also show that the buzz is modified to each capture situation, underlining the importance of the buzz for the present capture and not just for post-capture evaluation. This interpretation is corroborated by the acoustic behavior of odontocetes. DeRuiter *et al.* (2009) argue that continuation of the buzz after capture indicates a post-capture evaluation function, but the fact that the buzz rate increases until prey capture and falls off afterwards might also support the significance of the buzz for the present capture. The continuation of the buzz after capture, but at falling rates, might be caused by the click production mechanisms (Madsen *et al*. 2010).

The bat echolocation system is a model system for active perception which is superior to many other models, since it provides a window to scene analysis by recording the ongoing dynamic adaptation of echolocation signals to changing tasks and auditory scenes during prey pursuit. Another advantage of this model is that the acoustic gaze of the bat, i.e. the distance and direction where it focuses its sonar beam, gives a quantitative and direct measure of attention (Ulanovsky & Moss 2008). Studies of reaction time provide a useful approach to understanding the decision processes at the neural and behavioral level and the impact of attention. The reflex reactions like the startle response are much faster than what we have found in the prey removal trials, but making adaptive changes to a complex, multi-stage behavior involves further central processing and is therefore expected to require longer reaction times. Reaction times for other complex multi-stage behaviors in completely different systems tend to be longer than what we report here for echolocating bats. When *Drosophila* escapes from a black disk or a looming stimulus, the reaction time is around 200-300 ms (Card & Dickinson 2008a; Card & Dickinson 2008b; de Vries & Clandinin 2012). In a simple reflex (e.g. giant-fiber-evoked escapes of locusts), a stereotyped behavioral response is elicited when a command neuron fires a single action potential and is unaffected by further sensory input once the behavior has been initiated. In contrast, the reaction of *Drosophila* involves a ‘planning’ stage where wings are raised to prepare for flight and posture is adjusted to direct the animal away from the oncoming object. The behavior can be aborted at different stages, not unlike the reaction of the bats in our study. Also, stimulus elicited saccadic eye movements in humans have reaction times of around 200-250 ms, reflecting the integration of visual (bottom-up) information with cognitive (top-down) influences to select the eye movement that will maximise the input rate of task relevant visual information (Montagnini & Chelazzi 2005; Orban de Xivry & Lefevre 2007; Orban de Xivry *et al*. 2010; Spering & Montagnini 2011). The visual reaction time has been measured to around 200 ms by determining the oculomotor latency when humans adapt their secondary saccades to correct for movement of a visual target during the first saccade (Madelain *et al*. 2007; Panouillères *et al*. 2011). Such a situation approaches a visual parallel to the experiments performed here. However, we measured reaction times down to about 90 ms, much faster than those found in other non-reflex systems requiring higher order processing of sensory input like the visual experiments mentioned above. Such short reaction times can likely be achieved through echolocation since the temporal precision of the auditory system far exceeds that of other sensory modalities (Rabinowitz & King 2011). The short reaction times during echolocation that we measured in this study may indicate a strong evolutionary constraint for fast reaction. The relatively short detection ranges of echolocation in air (Jung *et al*. 2007; Surlykke & Kalko 2008; Brinkløv *et al*. 2010) could have created a need for speed as the bats must perform difficult perceptual evaluations under strong time pressure, such that the bats’ capture behavior is remarkable in its perceptual urgency to react on a very fast time scale.

4 General discussion

This study aimed to investigate the spatial and temporal resolution of bat sonar. Temporal analysis in echolocation can have two different meanings. On the one hand, temporal analysis can be understood as the temporal analysis of static spatial layouts. This is important when regarding a situation in which the bat as well as the surrounding objects are stationary and the bat has to analyze echoes from objects that are positioned at different distances relative to the bat. When the bat tries to focus on a target of interest in this situation, the detection of the target is impaired by forward and backward masking. On the other hand, temporal analysis can be understood as the echo-acoustic analysis of time-variant layouts. When the bat or the target is moving, the bat has to emit a series of echolocation calls to receive constantly updated information about the changing environment. In my thesis I addressed the temporal analysis of static spatial layouts as well as the echo-acoustic analysis of time-variant layouts.

In the first part of this thesis we quantified the spatio-temporal focus of bat sonar in a static spatial situation. This means we analyzed how well the bats are able to focus their echolocation system on a target echo and blend out masking echoes from surrounding objects that arrive at the same time at the bats' ears. We found that the spatial resolution of bat sonar is better than the auditory spatial resolution in humans, but much worse than the spatial resolution of the visual system (see below for a detailed discussion). Additionally, we quantified the bats' performance when the masking signals were temporally separated from the target signal (forward and backward masking). This corresponds to a situation in which the masking objects are spatially separated from the target and the distance between the bat and the masking objects is different from the distance between the bat and the target. In nature such a situation arises for example when a bat tries to detect an insect in front of background vegetation. When emitting an echolocation call, the bat will receive an echo from the insect and immediately afterwards echoes from the background vegetation that arise from different spatial positions. Because of the limited spatial resolution of their sonar system, bats might strongly profit from sequentially sampling their environment. By emitting a series of echolocation calls and varying the directional aim of the sonar beam or the position of their pinnae, bats might be able to spatially resolve surrounding objects more easily. In our experiments about the spatio-temporal focus of bat sonar the bats were not able to profit from sequential scanning as the masking objects were positioned symmetrically around the target.

An important aspect of echo-acoustic analysis of time-variant layouts is the rate at which bats acquire information about their environment. The higher the call repetition rate, the higher the temporal resolution with which the bat samples its environment. During search flight, bats emit echolocation calls with a repetition rate of 2 to 5 Hz. Between two calls the bats do not receive any information about their surroundings. During insect capture bats are faced with an extreme situation of time-variant echo analysis. Shortly before a bat catches the insect it emits calls at a rate of up to 200 Hz. This is called the terminal buzz. In the second part of this thesis we show that this high information acquisition rate allows for very fast adaptations in the bat's capture behavior. Insect capture in open space is one of the few situations in which the spatial resolution of bat sonar is not a crucial factor. Bats can even profit from lowering the frequency of their calls and thus broadening the emissions during the terminal buzz (Jakobsen & Surlykke 2010).

Thus, this study gives insights into the spatial resolution of bat sonar, the temporal analysis of static spatial layouts and the echo-acoustic analysis of time-variant layouts in bats. In the following the obtained results are discussed in more detail.

In the first part of this thesis, we quantified the spatio-temporal focus of the sonar system in the bat *P. discolor*. In a series of psychophysical experiments the bats had to detect a target in the presence of two maskers that were placed symmetrically around the target. When the angular separation between target and masker was increased from 8° to 40° in the simultaneous masking condition, the strength of masking decreased by 7 dB in the active-acoustic condition and by 6 dB in the passive-acoustic condition. Forward masking had a stronger effect on target detection than backward masking. Our results indicate that the use of active echolocation leads to a temporal sharpening of the spatio-temporal receptive field of *P. discolor*. Interestingly, we did not measure a complete release from masking, even with a target-masker separation of 40° or a temporal separation between target and masking signals of 6 ms. Our results indicate that most of the spatial selectivity of *P. discolor*'s sonar system stems from the spatial selectivity of the receiving subsystem. As bats emit echolocation calls with a much higher directionality in the field than in the laboratory (Surlykke *et al*. 2009), the contribution of the emitting system to the spatial selectivity of the whole sonar system might be higher in the field than in our experiments.

The rather poor spatial resolution in echolocating bats in this study might be surprising at first glance, as many studies have demonstrated very high spatial acuity in the auditory system. Auditory spatial acuity can be investigated by measuring minimum audible angle (MAA) thresholds in a psychophysical paradigm in which two successive stimuli are presented at different spatial positions and the test subjects have to indicate whether the second stimuli appeared to be left or right (horizontal plane) or up or down (vertical plane) relative to the first stimulus. The MAA under optimum conditions in humans is about 1° in the horizontal plane (Mills 1958; Grantham 1986; Perrott & Saberi 1990; Grantham *et al*. 2003) and 4° in the vertical plane (Perrott & Saberi 1990; Grantham *et al*. 2003). It has been shown that different mechanisms are responsible for horizontal and vertical localization. Spectral differences that stem from the directional filtering of the pinnae allow for spatial positioning in the vertical plane and interaural time differences (ITDs) and interaural intensity differences (IIDs) enable spatial positioning in the horizontal plain (Moore 2008).

Horizontal spatial acuity in passive sound localization has also been measured in five different bat species: *Eptesicus fuscus, Rousettus aegyptiacus, Artibeus jamaicensis, Phyllostomus hastatus* and *Carollia perspicillata*. The MAA ranged between 9° and 15° for these five bats species (Koay *et al*. 1998; Heffner *et al*. 1999; Heffner *et al*. 2001; Heffner *et al*. 2007). Heffner *et al.* (2007) showed that the MAAs of these bats lie in the middle of the MAA distribution for other mammals, which rages from about 1° to more than 50° and has a mean of 12°. In an active echolocation task, the bat *E. fuscus* was even able to discriminate horizontal angular differences of 1.5° (Simmons *et al*. 1983). While most mammals seem to use ITDs (which are well suited for localization at high frequencies) as well as IIDs (which are well suited for localization a low frequencies), it has been shown that some bat species (*E. fuscus, P. hastatus* and *C. perspicillata*) are not able to use ITDs for localization (Koay *et al*. 1998; Heffner *et al*. 2010). *R. aegyptiacus* and *A. jamaicensis*, in contrast, are able to localize targets based on ITDs (Heffner *et al*. 1999; Heffner *et al*. 2001).

Auditory spatial acuity, however, is fundamentally different from auditory spatial resolution. While auditory spatial acuity describes the ability to localize a test stimulus relative to a reference stimulus that was presented before the test stimulus, auditory spatial resolution describes the ability to detect a stimulus while other stimuli are presented simultaneously at different spatial locations.

Binetti (2009) conducted experiments that indicate that the auditory spatial resolution in humans is very bad. The subjects had to detect a target signal (band pass filtered noise) in the presence of two symmetrically arranged masking signals (band stop filtered uncorrelated noise). Even at an angular separation between target and masker of 90° no spatial unmasking could be observed. This indicates that the auditory space in humans consists of two broad spatial receptive fields that cover one hemisphere each. This finding is supported by a study of Boehnke and Phillips (1999), in which the tuning of spatial channels in humans was determined, indicating one spatial channel for each lateral hemifield. In the current study spatial unmasking effects of 7 dB in the active-acoustic and 6 dB in the passive-acoustic experiment were measured for an increase of angular separation between target and maskers from 8° to 40° in the bat *P. discolor*. Thus, the auditory spatial resolution seems to be better in *P. discolor* than in humans. However, in humans as well as in bats the rather bad auditory spatial resolution contrasts with a very good auditory spatial acuity.

The distinction between positional acuity and resolution is also important in the visual system. To analyze visual resolution it is typically tested how close two adjacent structures can be so that they are still perceived as separate. Another possibility is to use spatial sinusoidal gratings and measure the highest spatial frequency (i.e. how fine the pattern can be) at which the pattern can still be perceived. The resolution limit of the human eye is in the order of 1 min of arc (= 1/60 of 1°) (reviewed in Westheimer 1976; Westheimer 1987).

To measure positional acuity, on the other hand, subjects have to judge the position of one structure relative to other structures (e.g. Vernier alignment test). It is important to note that positional acuity in vision is usually measured in a simultaneous paradigm while auditory spatial acuity is generally measured in a sequential paradigm. In vision, positional acuity thresholds as low as about 2 sec of arc have been reported (reviewed in Westheimer 1976; Westheimer 1987). Positional acuity is much better than visual resolution because in contrast to localization of a one point source, resolution of a two point source is limited by diffraction (reviewed in Westheimer 1976; Westheimer 1987).

Perrott *et al.* (1993) compared auditory and visual acuity using a sequential paradigm for both senses. For a frontal presentation of the reference stimulus, the MAA was about 1° and the minimum visual angle (MVA) about 0.5° (27 min of arc). In peripheral regions localization performance decreased for both senses, but in contrast to the frontal presentation, MAA thresholds were lower than MVA thresholds. This shows that visual acuity is not substantially better than auditory acuity.

Visual resolution and auditory resolution are hard to compare as different experimental paradigms have been used. However, visual resolution seems to be much better than auditory resolution. The rather bad auditory spatial resolution in our experiments might support the hypothesis of Noble and Perrett (2002) that spatial hearing in an animal with frontally oriented vision is mainly needed to draw the attention of the animals to events outside the current field of view. For objects within the immediate field of view vision and not hearing may mainly be used to resolve individual objects. It is interesting that auditory spatial resolution in an echolocating bat, which is able to navigate through complex environments without using vision, but relying exclusively on echolocation, is also rather bad. This is not as surprising, however, when one takes into consideration that the auditory system of bats is basically a typical mammalian auditory system (Suga 1990; Moss & Surlykke 2010). Furthermore, it has been shown, that bats use vision for spatial orientation and foraging (Masterso & Ellins 1974; Buchler & Childs 1982; Bell 1985; Bell & Fenton 1986; Eklöf & Jones 2003; Zhao *et al*. 2009). Heffner and Heffner (1992) showed that in different mammalian species, high auditory localization acuity correlates with a narrow field of best vision and low auditory localization acuity correlates with a broader field of best vision. This correlation also holds true for the passive sound localization performance of five bat species. Thus, also bats might react to external sounds by directing their field of best vision towards the sound source (Heffner *et al*. 2007).

However, in complete darkness bats cannot use their visual system to obtain information about their environment. When using active echolocation, differences e.g. in spectral composition and delay of echoes from different objects might help the bat to spatially resolve those objects. Dynamic scene analysis is probably very important in the perception of complex, dynamic environments by bats. Moss and Surlykke (2010) hypothesized that bats group echoes of different objects into perceptual streams in order to facilitate the segregation of these auditory objects. A bat that echolocates in a complex environment receives a multitude of echoes from different sonar targets at each emitted echolocation call. If bats perceptually group the echoes of specific objects across adjacent echolocation calls, sequential scene analysis processes might lead to different perceptual streams for the different sonar targets. The echoes might be grouped according to their direction, timing (call-echo delay), intensity, frequency and duration (Moss & Surlykke 2010). The results of the current study show that the spatial resolution in *P. discolor* is rather poor and that timing and direction are not independent factors. This indicates that the extent to which echoes can be attributed to different objects according to their direction and timing is limited. Thus, for bats to form auditory objects, it might be important that differences in target strength, spectral composition of the echoes and echo duration are present in addition to differences in direction and timing.

In the second part of this thesis, we investigated temporal resolution of bat sonar in the context of echo-acoustic analysis of time-variant layouts. As bats ensonify their environment discontinuously (in search flight often only every 200-500 ms, corresponding to a call emission rate of 2 - 5 Hz), they are not able to gather any information about their environment in between two sonar emissions and cannot react immediately to sudden changes during this time. During insect capture, where it is essential for bats to adjust their behavior to rapid changes in the prey's flight path, bats emit echolocation calls at a much higher rate (up to 200 Hz during the terminal buzz). We investigated if the bats' temporal resolution during the terminal buzz is high enough to compensate for any disadvantage in reaction time that bats might face due to the stroboscopic nature of echolocation. Our experiments showed that neither the echolocation nor the capture behavior of the bats during the terminal phase is an "all-or-nothing" behavior, but that buzz 2 is shortened when the prey is removed earlier than 100 ms before expected capture and the capture behavior can be changed even when the prey is removed immediately before expected capture. The reaction time of the bats in this study, measured from the time of prey removal to the abortion of the bats' echolocation or capture behavior, was in the order of 100 ms. Additionally, we measured the latency of the acoustic startle response in the three bats that took part in the laboratory experiments. The acoustic startle response is a reflex-like behavior that involves a simple neuronal pathway in the ponto-medullary brainstem (Koch 1999). The latency of the acoustic startle response in *M. daubentonii* was about 20 ms in our experiments. This result is in the same order of magnitude as latencies of the acoustic startle response measured in rats, which are about 10 ms (Cassella *et al*. 1986; Caeser *et al*. 1989; Koch 1999). In humans, the latency of the acoustic startle response, recorded in the orbicularis oculi muscle, is about 60 ms. However, the auditory blink reflex which is mediated by a different neuronal pathway has shorter latencies (Koch 1999).

These short reaction times down to less than 10 ms contrast with the bats' reaction time of about 100 ms measured from prey removal to the abortion of capture-related behavior in this study. However, the abortion of a complex capture behavior is not a reflex-like behavior but requires higher order processing. Thus, reaction times are expected to be longer than in reflex-like behaviors. Reaction times have also been measured in complex multi-stage behaviors in completely different systems. Drosophila escaping from a black disk or a looming stimulus had reaction times of about 200-300 ms (Card & Dickinson 2008a; Card & Dickinson 2008b; de Vries & Clandinin 2012) and saccadic eye movements in humans revealed reaction times of about 200 ms (Madelain *et al*. 2007; Panouillères *et al*. 2011). Reaction times were also measured in humans in animal detection tasks that involve high level object recognition. In these experiments pictures were briefly presented to the subjects and the subjects had to respond (by pressing a mouse button) if the picture showed a target category (e.g. an animal).

Non-target pictures showed for example landscapes, buildings or flowers. Minimum reaction times were about 250 ms (Thorpe 2002). Similar experiments have been conducted with monkeys and minimum reaction times for the categorization of natural images were between 160 and 180 ms (Fabre-Thorpe *et al.* 1998; Thorpe 2002).

The bats' reaction time of about 100 ms is rather short compared to the reaction times in these other complex multi-stage behaviors. This means that bats seem to overcome the problem of stroboscopic active sensing by emitting echolocation calls at a very high rate during the terminal buzz. This very high temporal resolution of echolocation during the terminal buzz enables the bats to successfully track and catch flying insects in complete darkness via echolocation.

As bats emit echolocation calls with a repetition rate of up to 200 Hz during the terminal buzz, the question arises if the temporal resolution of the bats' auditory system is high enough to perceive each call of the buzz as a separate event.

In the visual system the temporal resolution limit can be analyzed by measuring the flicker-fusion frequency, the frequency at which an intermittent light stimulus can no longer be discriminated from a continuous one. In humans flicker-fusion frequencies between about 20 and 60 Hz have been measured (Kelly 1972; Zanker & Harris 2002).

In the auditory system temporal resolution can be assessed by measuring how high the modulation frequency of an amplitude modulated stimulus can be, so that the auditory nervous system can still follow the amplitude modulation. Mooney *et al.* (2009) assessed the auditory temporal resolution of a white-beaked dolphin and compared their results with other studies that analyzed the auditory temporal resolution of odontocetes and other mammals. To allow for a comparison between different species, they used studies in which amplitude modulated stimuli were utilized and responses with auditory evoked potentials recorded from brainstem activity were measured. However, as the auditory evoked potentials from gerbils and humans contain not only brainstem evoked potentials but also cortical components, the comparison has to be handled with care (Dolphin & Mountain 1992; Purcell *et al.* 2004; Mooney *et al.* 2009). The temporal resolution limit was between 1150 Hz and 1450 Hz for odontocetes (data from Supin & Popov 1995; Szymanski *et al.* 1998; Klishin *et al.* 2000; Cook *et al.* 2006; Mooney *et al.* 2006; Mooney *et al.* 2009, Pseudorca crassidens (unpublished)), between 220 Hz and 750 Hz for pinnipeds (data from Mulsow & Reichmuth 2007), between 160 Hz and 1400 Hz for manatees (data from Mann *et al.* 2005), between 48 Hz and 200 Hz for gerbils (data from Dolphin & Mountain 1992) and between 42 Hz and 60 Hz for humans (data from Purcell *et al.* 2004). It was also shown that free-tailed bats are

probably able to follow amplitude modulations up to 500 Hz (Grothe *et al*. 1997). Thus, echolocating bats and odontocetes have a high temporal resolution and Mooney *et al.* (2009) hypothesize that echolocation might have been an important factor that lead to the high auditory temporal resolution. It is important to note that the reported temporal resolution limits depend strongly on the experimental method. For example a behavioral experiment showed that, in contrast to the results cited above, gerbils were able to follow amplitude modulations up to 1000 Hz (Wiegrebe & Sonnleitner 2007).
It can be concluded that during the terminal buzz, when echolocation calls are emitted at repetition rates up to 200 Hz, bats can probably still perceive each call as an individual event. However, when the bat is very close to the prey, the echo delay time is very short and call and echo might interact in the bat's perception.

To sum up, in most mammals the spatial acuity of the visual as well as of the auditory system is very high while the spatial resolution seems to be much worse, especially in the auditory system. The temporal resolution of the auditory system, on the other hand, is thought to be very high. While this study indicates that the spatial resolution of bat sonar is better than the spatial resolution of the human auditory system, it also shows that it is likely that bats heavily rely on additional cues (like differences in frequency content and echo delay) to successfully navigate through a complex environment. This study also shows that the temporal resolution of bat sonar during the terminal buzz is high enough to allow for a very rapid update of information and thus enabling very fast adaptations to changes in the environment.

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Eidesstattliche Versicherung

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation “Spatial and temporal resolution of bat sonar” selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

München, den

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Author contributions

Spatio-temporal focus of bat sonar:

Lutz Wiegrebe and Cornelia Geberl designed the experiments and the analysis. Cornelia Geberl wrote the experimental programs, collected the data of the active-acoustic experiments (except the condition with a masker position of 40° and a signal delay -6 ms), conducted the analysis and wrote the manuscript. Cornelia Geberl and Lutz Wiegrebe supervised the diploma thesis of Kathrin Kugler and the thesis (Zulassungsarbeit) of Daniela Tietz. For their theses, Kathrin Kugler and Daniela Tietz collected the data of the passive-acoustic experiments and of the condition with a masker position of 40° and a signal delay -6 ms in the active-acoustic experiment. The program for the illustration of the synthetically produced echolocation call was written by Kathrin Kugler. Cornelia Geberl implemented the simulation of the experiment by adapting the auditory model of bat sonar that was conceived by Lutz Wiegrebe.

What's the buzz? Sensory-motor coupling during high-speed echolocation in bats:

This project was conducted in close collaboration with Signe Brinkløv and Annemarie Surlykke, University of Southern Denmark. Annemarie Surlykke and Signe Brinkløv designed the laboratory experiments. Data collection and analysis of raw data for the laboratory experiments was done by Signe Brinkløv. Lutz Wiegrebe and Cornelia Geberl designed the field experiments and the data analysis. Thomas Dera customized the EyeSeeCam program to implement a real time positioning of bats for the field experiments. Cornelia Geberl collected as well as analyzed the data of the field experiments and conducted all statistical analysis. Marc Sieber assisted Cornelia Geberl in the data collection for the field experiments. Figures 3.2 and 3.5 were designed by Singe Brinkløv while the remaining figures were designed by Cornelia Geberl. The manuscript was written by Cornelia Geberl, Annemarie Surlykke, Signe Brinkløv, and Lutz Wiegrebe.

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