# PSYCHOPHYSICAL EXPERIMENTS ON SOUND LOCALIZATION IN STARLINGS AND HUMANS

von

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### Abstract

The localization of sound sources represents one of the major challenges to the auditory system and affects an animal's survival or reproduction. Comparisons of results across previous sound localization studies allow identifying generalized principles in the underlying processing mechanisms. However, in such comparisons it is often assumed that the specific method used to measure sound localization does not influence results. In this dissertation, I present psychophysical experiments on sound localization in starlings and in humans which showed that often unexpressed differences between methods complicate the comparison of results across previous studies.

In the first part of this dissertation, I provide an overview of differences between established paradigms used to study the localization of static sound sources. I present experiments on sound localization in the European starling (Sturnus vulgaris) which investigated the effect of stimulus repetitions on sound localization (Experiment I) and revised the traditional classification of sound localization paradigms (Experiment III). Furthermore, Experiments I-III establish the starling as a suitable animal model for sound localization. Experiment I measured sound localization relative to an acoustic reference. A repeated standard stimulus was replaced by a test stimulus from another position. Starlings were trained to detect this switch in sound source position. An improvement in sound localization with an increasing number of standard stimulus presentations indicated that stimulus repetitions enhanced the internal spatial representation of a sound source. Thus, stimulus repetitions may have affected results reported in a large number of previous sound localization studies. In Experiment II, the starling head turns in video recordings from *Experiment I* were analyzed. Starlings turned their heads during the presentation of sounds with long durations. These head turns improved sound localization. Experiment III revised the traditional classification of sound localization paradigms by introducing a new paradigm: sound localization relative to a non-acoustic reference. In this experiment, starlings were trained to indicate whether a stimulus was presented from the left or from the right. The experiment measured localization of the sound source relative to the non-acoustic transition point between "left" and "right". The revised classification of sound localization paradigms has broad implications for interpreting results from previous studies with similar paradigms.

In the second part of this dissertation, I focus on the representational momentum effect (RM). This effect describes that in humans, the perceived endpoint of a moving target is displaced in the direction of the target's movement. Many previous studies showed that RM increases with target velocity in the visual modality. However, the few previous studies investigating the effect of target velocity on RM in the auditory

modality found ambiguous results. I discuss potential disadvantages in methods used to study auditory RM which may explain this difference in findings between visual and auditory RM studies. *Experiment IV* investigated the effect of target velocity on auditory RM while avoiding these potential disadvantages in methods. Auditory RM linearly increased with target velocity, which is in line with the findings on visual RM. This suggests that similar mechanisms underlie RM in the two modalities.

In summary, this dissertation identifies how methods may affect results in studies on the localization of static sound sources and on auditory RM. I introduce a guideline which specifies how to avoid many disadvantages in the methods and how to interpret results from previous studies. This improves the comparability of results across studies on sound localization.

### ZUSAMMENFASSUNG

Die Lokalisation von Schallquellen stellt eine der größten Herausforderungen für das auditorische System dar und beeinflusst das Überleben und die Fortpflanzung von Tieren. Vergleiche von Ergebnissen zwischen früheren Studien zur Schalllokalisation erlauben, generelle Prinzipien in den zugrunde liegenden Prozessen zu identifizieren. In solchen Vergleichen wird jedoch häufig angenommen, dass die spezifische Methode in den Studien zur Untersuchung der Schalllokalisation die Ergebnisse nicht beeinflusste. In dieser Dissertation stelle ich psychophysikalische Experimente zur Schalllokalisation bei Staren und Menschen vor, die zeigten, dass oftmals unerwähnte Unterschiede zwischen diesen Methoden den Vergleich von Ergebnissen zwischen früheren Studien erschweren.

Im ersten Teil dieser Dissertation gebe ich einen Überblick über Unterschiede zwischen etablierten Paradigmen, die in Studien zur Lokalisation unbewegter Schallquellen genutzt werden. Ich stelle Experimente zur Schalllokalisation beim Star (Sturnus vulgaris) vor, die den Einfluss von Reizwiederholungen auf die Schalllokalisation untersuchten (Experiment I) und die traditionelle Klassifikation von Paradigmen zur Schalllokalisation revidierten (Experiment III). Darüber hinaus wird der Star mit den Experimenten I-III als Tiermodell für Schalllokalisation etabliert. Experiment I maß die Lokalisation einer Schallquelle relativ zu einer akustischen Referenz. Ein wiederholter Standardreiz wurde durch einen Testreiz von einer anderen Position ersetzt. Die Stare wurden darauf trainiert, diesen Wechsel in der Schallquellenposition zu detektieren. Eine Verbesserung der Schalllokalisation mit steigender Anzahl an Standardreizen deutete darauf hin, dass Reizwiederholungen die interne räumliche Repräsentation von Schallquellen verbesserten. Somit könnten Reizwiederholungen die Ergebnisse einer Vielzahl an früheren Studien zur Schalllokalisation beeinflusst haben. In Experiment II wurden die Kopfbewegungen der Stare in Videoaufnahmen von Experiment I analysiert. Die Stare bewegten ihren Kopf während der Präsentation von lang andauernden Reizen. Diese Kopfbewegungen verbesserten die Schalllokalisation. Experiment III revidierte die traditionelle Klassifikation von Paradigmen zur Schalllokalisation, indem es ein neues Paradigma einführte: die Schalllokalisation relativ zu einer nicht-akustischen Referenz. In diesem Experiment wurden Stare darauf trainiert, anzuzeigen, ob ein Stimulus von links oder von rechts präsentiert wurde. Das Experiment maß die Lokalisation der Schallquelle relativ zu dem nicht-akustischen Übergangspunkt zwischen "rechts" und "links". Die revidierte Klassifikation von Paradigmen zur Schalllokalisation hat große Bedeutung für die Bewertung von Ergebnissen in früheren Studien, in denen ähnliche Paradigmen verwendet wurden.

Im zweiten Teil dieser Dissertation behandle ich den "representational momentum effect" (RM). Dieser Begriff beschreibt, dass die Wahrnehmung des Menschen die

letzte Position eines bewegten Reizes in Richtung der Reizbewegung verschiebt. Viele frühere Studien zeigten, dass im visuellen Sinn der RM mit der Reizgeschwindigkeit ansteigt. Im Gegensatz dazu zeigten die wenigen früheren Studien zum Einfluss der Reizgeschwindigkeit auf den RM im auditorischen Sinn mehrdeutige Ergebnisse. Ich diskutiere mögliche Nachteile in Methoden von Studien zum RM im auditorischen Sinn, die diesen Unterschied in den Ergebnissen zwischen Studien zum visuellen und zum auditorischen RM erklären könnten. Experiment IV untersuchte den Einfluss der Reizgeschwindigkeit auf den RM im auditorischen Sinn, während es diese möglichen Nachteile in den Methoden vermied. Der RM stieg linear mit steigender Reizgeschwindigkeit an, was den Ergebnissen zum RM im visuellen Sinn entspricht. Somit könnten ähnliche Mechanismen dem RM in beiden Sinnen zugrunde liegen.

Zusammenfassend zeigt diese Dissertation auf, wie Methoden die Ergebnisse in Studien zur Lokalisation unbewegter Schallquellen und zum RM im auditorischen Sinn beeinflussen können. Ich stelle einen Leitfaden zur Vermeidung vieler Nachteile in den Methoden und zur Bewertung von Ergebnissen früherer Studien vor. Dies verbessert die Vergleichbarkeit von Ergebnissen zwischen Studien zur Schalllokalisation.

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## ABBREVIATIONS

2AFC	two-alternative forced choice	
ALPM	absolute loudspeaker position method	
CN	cochlear nucleus	
GLMM	Generalized Linear Mixed Model	
HRTF	head-related transfer function	
IC	inferior colliculus	
IID	interaural intensity difference	
ITD	interaural time difference	
LPM	loudspeaker pair method	
ΜΑΑ	minimum audible angle	
MRA	minimum resolvable angle	
NL	nucleus laminaris	
p(c)	probability of correct response	
PMF	psychometric function	
RM	representational momentum effect	
SC	superior colliculus	
SDT	signal detection theory	
SOC	superior olivary complex	
VAS	Virtual Auditory Space	

### **1.** INTRODUCTION

Localizing sound sources is a key ability which ensures survival in the natural environment for many species, for example in predator-prey and territorial interactions (e.g., Klump 2000). Unlike the spatially restricted field of view, the auditory sense allows monitoring all spatial directions. Often, localization of sounds results in the orienting of the animal's eyes, head and body towards the source (e.g., Nodal et al. 2008). Even more than 100 years after Lord Rayleigh (Strutt 1907) proposed the duplex theory of sound localization that hypothesizes that the azimuthal localization of auditory events relies on binaural cues, the knowledge about internal representation of sound source positions remains imprecise (e.g., Ashida & Carr 2011; Ahveninen et al. 2014) and is "currently a hot topic" (Ahveninen et al. 2014, p.89).

More fundamental research on the processing of sound source positions is mandatory and requires the use of animal models (e.g., Hausmann & Wagner 2011). The first part of this dissertation characterizes sound localization on the behavioural level in the European starling (Sturnus vulgaris), a non-specialized bird that represents a wellestablished animal model in the auditory modality (Klump et al. 2000). Despite an evolutionary distance of about 300 million years (e.g., Grothe et al. 2010; Köppl 2011), similar evolutionary requirements have resulted in striking auditory processing parallels between humans and starlings (Klump et al. 2000). Among others, these comprise vocalization and learning (Eens et al. 1991) and frequency selectivity (Langemann et al. 1995). In addition to these similarities in auditory processing, experimenters can easily train starlings in reinforced behavioural paradigms (e.g., Feinkohl & Klump 2011), and the species is suited well for neurophysiological experiments (e.g., Itatani & Klump 2009). By measuring the binaural cues available to the auditory system of starlings, Klump & Larsen (1992) provided an important basis for my psychophysical studies on sound localization in this species. In the first part of this dissertation, I will measure sound localization thresholds in this animal and analyse the effect of head turns on thresholds (Experiment I of this thesis: Feinkohl & Klump 2013; Experiment II of this thesis: Feinkohl et al. 2013; Experiment III of this thesis: Feinkohl et al. 2014).

A large number of studies have investigated sound localization processing on the behavioural level. Two of the most important goals are a characterization of the ability to localize sound as a prerequisite for interpreting neuronal activity in sound localization tasks (e.g., Bala et al. 2003), and a comparison between studies and species to identify general rules (e.g., the relationship between sound localization thresholds and the width of the field of best vision, see Heffner 1997). Such goals require close attention to the individual tasks and stimulus presentations in each study. However, despite a multitude of procedures that are used to study sound

localization, even most psychoacoustic textbooks do not provide detailed discussions of methods in sound localization experiments (Letowski & Letowski 2012). The major focus of the first part of this dissertation is to provide an overview over common yet often unexpressed differences between sound localization studies that should be taken into account when comparing results (Chapter 3 of this dissertation). One effect that has not yet been investigated is the role of stimulus repetitions that are often employed in sound localization studies (e.g., Heffner & Heffner 1988; Recanzone et al. 1998; Bala et al. 2003). I will present an experiment that focuses on the effect of stimulus repetitions on sound localization thresholds (Experiment I of this dissertation: Feinkohl & Klump 2013) and discuss implications for interpreting results from corresponding studies. Another focus of the first part of this dissertation lies on the traditional concept that all sound localization experiments are limited to two types of task (e.g., Moss & Carr 2012): either subjects report the absolute sound source position (e.g., Carlile et al. 1997), or they localize a sound relative to a second sound source position (e.g., Mills 1958). I will present a study that challenges this traditional view (Experiment III of this thesis: Feinkohl et al. 2014). In the experiment, subjects localize a sound source relative to a non-acoustic reference, and I discuss the implications for analysing and interpreting results from studies with similar paradigms. I will also suggest a standardization of methods in experiments on relative localization that reduces potential influences of procedures on thresholds and improves the comparability of results between corresponding sound localization studies.

The cues available to the auditory system for static sound localization also represent the basis for the auditory motion perception system. Similar to the processing of stationary sounds, the mechanisms of this system are subject to an ongoing discussion (Deas et al. 2008; Letowski & Letowski 2012). A prominent example is the processing underlying the auditory representational momentum effect (RM): subjects that are asked to report the endpoint of a moving sound source mislocalize this endpoint towards the trajectory of motion. RM has also been described in the visual modality, and a large number of studies have provided insight into the variables influencing visual RM and theories underlying this effect (for reviews, see Hubbard 2005; Hubbard 2010). Similar effects between visual and auditory RM would allow auditory motion research to benefit from this large body of knowledge. Many studies on visual RM have shown an increase in RM size with an increase in target velocity (e.g., Hubbard & Bharucha 1988; see Hubbard 2005). However, the scarce number of previous studies on the effect of target velocity on auditory RM yielded ambiguous results (Perrott & Musicant 1977; Getzmann et al. 2004; Schmiedchen et al. 2013). The second part of this dissertation discusses potential disadvantages in the methods employed in previous studies on auditory RM (Chapter 4 of this dissertation). I will present an experiment on auditory RM that avoids these potential disadvantages of previous studies to provide an unbiased measure of the effect of target velocity on auditory RM (Experiment IV of this thesis: Feinkohl et al. 2014).

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# 2. PROCESSING OF SOUND SOURCE POSITION: A SHORT OVERVIEW

In the following, I will provide a brief overview of cues that are used to localize sound and of the neuronal processing involved in the localization of stationary and moving sound sources. Then, I will briefly discuss the influence of stimulus duration and spectrum on the localization of sounds.

### 2.1. Sound localization cues

Unlike the retina in the visual system, the primary receptors of the auditory system do not obtain information about stimulus position. Hair cells on the cochlear basilar membrane code the input tonotopically, i.e. along a frequency gradient (e.g., Grothe et al. 2010). With substantial processing (e.g., Carlile et al. 2005; Ahveninen et al. 2014), the auditory system derives spatial information from two types of cues: binaural cues resulting from the spatial distance between the two ears, and monaural cues resulting from acoustic filtering of the sound before it reaches the inner ear (e.g., Carlile et al. 2005).



**Figure 2.1**: Binaural and monaural cues used for sound localization. a) For sound sources off the midline, the distance travelled by the sound before reaching the ear differs between the left and the right ear, indicated by  $d_{left}$  and  $d_{right}$ , respectively. This results in the interaural time difference (ITD) that represents a binaural cue for the azimuthal sound source position. b) The head shadowing of the sound waves results in the interaural intensity difference (IID) that represents a binaural cue for the azimuthal sound waves with the ear, head and torso result in stimulus spectra reaching the eardrum specific to the elevation of the sound source position (adapted from Grothe et al. 2010).

The interaural time difference (ITD) represents a binaural cue that is defined by the difference in the time the sound travels from the sound source until it arrives at the two ears (Figure 2.1a). It is largest for sound sources at  $\pm 90^{\circ}$  azimuth, reaching about 700 µs in humans (e.g., Middlebrooks & Green 1991) and about 100 µs in starlings (Klump & Larsen 1992). This cue is transmitted to the brain by hair cells phase-locking activity to the sound waves. The refractory period of the inner hair cells in mammals and starlings limits the use of this binaural cue to frequencies below about 2 kHz (e.g., Gleich & Narins 1988; Köppl 1997; Grothe et al. 2010).

The interaural intensity difference (IID), another binaural cue for sound localization, results from the head shadowing effect (Figure 2.1b): the head attenuates the sound waves travelling to the ear contralateral to the sound source, which leads to a difference in sound pressure level reaching the two ears. The IID is larger for lateral than for frontal angles (e.g., Shaw 1974; Macaulay et al. 2010). The wavelengths of the sound determine the amount of attenuation, with high frequency sounds resulting in a larger attenuation. The human head significantly affects IID for frequencies above about 1 kHz (e.g., Middlebrooks & Green 1991; Macaulay et al. 2010). In starlings, Klump & Larsen (1992) showed that the IID for frontal sound sources deviates from the IID for lateral sound sources at frequencies greater than about 2 kHz (Figure 2.2).



**Figure 2.2:** Sound pressure at the auditory meatus of the starling's right ear, for sound sources from -180° to +180° azimuth and 0° elevation (adapted from Klump & Larsen 1992). Medians of 6 to 7 measurements on 3 birds are normalized to the frontal position.

The symmetry of the head results in ambiguous binaural cues. Each combination of ITD and IID does not represent a single position in space, but a range of positions on the "cone of confusion" (e.g., Carlile et al. 2005). To resolve this ambiguity, the auditory system can use monaural cues to analyse the elevation of the sound source (Figure 2.1c): each sound source position results in a specific spectral profile, the head-related transfer function, due to interactions of the sound waves with the ear, the head and the torso (e.g., Carlile 1996; Letowski & Letowski 2012). This spectral filtering allows the auditory system to reconstruct the elevation of the sound source. The auditory

system combines these monaural cues with the binaural cues that define the azimuth of the sound source to form an unambiguous sound source position.

Unlike humans, birds possess an interaural canal, an air-filled cavity connecting the tympanic membranes of the two ears. The resulting directional pattern of the tympanic vibration amplitudes resembles an interaction between directional cues and the sound transmission path (e.g., Klump 2000; Michelsen & Larsen 2008). The influence of the interaural canal on sound localization is still under debate (e.g., Klump 2000; Michelsen & Larsen 2008; Köppl 2009; Christensen-Dalsgaard 2011), but theoretical models and current findings in lizards suggest that it increases the binaural cues (e.g., Köppl 2009; Christensen-Dalsgaard 2011). Measurements of the effect of the interaural canal on tympanic vibration in birds, including the European starling (Klump & Larsen 1992), led to ambiguous results that may be related to disadvantages associated with the specific methods employed (e.g., Klump 2000; Michelsen & Larsen 2008; Köppl 2009; Christensen-Dalsgaard 2011).

### 2.2. NEURONAL PROCESSING OF SOUND SOURCE POSITION

The representation of the position of auditory signals in mammals (for recent reviews, see Grothe et al. 2010; Letowski & Letowski 2012) begins with the transformation of mechanical sound energy into neuronal activity. Sound waves reaching the ear cause the eardrum to vibrate, and middle ear bones, the ossicles, transmit these vibrations to the fluids in the cochlea. Stereocilia of hair cells along the cochlea are deflected by vibrations of the cochlea, which generates action potentials that are transmitted to the brain via the auditory nerve. Auditory nerve axons terminate in the cochlear nucleus (CN) in the central nervous system that analyses temporal and spectral information. The CN projects to the ipsilateral and contralateral superior olivary complex (SOC) as well as to the ipsilateral and contralateral inferior colliculus (IC) that also gets input from the SOC. With the crossing of the midline, the SOC receives and passes on azimuthal positional information. The IC is the final processing stage for directional information in the brainstem. It combines the binaural cues from the SOC with the monaural cues from the CN. It projects to the superior colliculus (SC), a site for multimodal integration with a topographical representation of audiovisual space (e.g., Stein & Stanford 2008). The IC also projects to the medial geniculate body that connects to the auditory cortex where the perception of auditory objects is formed.

In the avian processing of sound source position (illustrated in Figure 2.3), parallel pathways analyse ITD and IID (e.g., see Klump 2000; Konishi 2000; Singheiser et al. 2012). In the afferent ITD pathway, auditory nerve signals reach the nucleus magnocellularis that projects bilaterally to the nucleus laminaris (NL). The NL processes time differences through a place code with delay lines and coincidence detectors

equivalent to the Jeffress model (see Jeffress 1948; e.g., Grothe et al. 2010; Ashida & Carr 2011; Macleod & Carr 2012). Its axons connect contralaterally to the anterior part of the ventral lateral lemniscus (LLDa, previously referred to as VLVa) and to the IC. In the afferent pathway that processes IID, the auditory signal first reaches the nucleus angularis and is then transmitted contralaterally to the posterior part of the ventral lateral lemniscus (LLDp, previously referred to as VLVp) and to the IC. ITD and IID pathways converge in the IC that comprises space-specific neurons. The IC projects to the optic tectum that forms a multimodal space map. Axons from the IC also connect to the nucleus ovoidalis that projects to Field L, a primary forebrain auditory area.



**Figure 2.3:** Pathways for avian ITD and IID processing (modified after Klump 2000; Konishi 2000; Singheiser et al. 2012). To clarify, not all connections are shown, and connections are based on auditory nerve signals from one ear. Nuclei coloured in blue transmit ITD information, nuclei coloured in yellow transmit IID information. Processing of both binaural cues converges in the inferior colliculus that is coloured in green. For details, see text.

Spatially dynamic conditions are common for sounds in the natural environment, for example if the sound source moves relative to the observer. Motion perception can aid for example in the detection of camouflaged predators and the prediction of object paths (e.g., Wagner et al. 1997). In contrast to research on visual motion processing (for current review, see Nishida 2011), the neuronal processing that underlies auditory motion perception is still not well understood. Auditory motion research has

established two competing hypotheses and identified evidence for both, but the specific mechanisms are still a matter of debate (e.g., Deas et al. 2008; Letowski & Letowski 2012). The snapshot hypothesis (Grantham 1986) proposes successive comparisons of object positions over time. The motion detector hypothesis (Perrott & Marlborough 1989; Perrott et al. 1993) proposes neurons directly responding to motion. In my view, the snapshot and the motion detector hypotheses do not appear to be mutually exclusive. Moving sound sources change their position in space over time. The nervous system underlies a sample rate (e.g., the maximum rate of action potentials), so the processing of object motion should be based on the comparison of successive object positions. Vice versa, the perception of motion requires neurons responsive to motion. Therefore, I believe that a snapshot process and motion detectors may coexist in the auditory system.

#### 2.3. INFLUENCE OF STIMULUS DURATION AND SPECTRUM ON LOCALIZATION

In sound localization experiments, stimulus duration is classified as either "open-loop" or "closed-loop" (e.g., Klump 2000). Under open-loop conditions, stimuli terminate before the subject can initiate head turns in response to the sound. Stimuli presented under closed-loop conditions allow for head turns during the presentation of the sound. In closed-loop stimuli, head turns improve sound localization in humans and other mammals (e.g., Perrett & Noble 1997; Tollin et al. 2005; Populin 2006) and may serve to orient the area of highest auditory spatial resolution towards the sound source (e.g., Middlebrooks & Green 1991). Even without active head movements, long stimulus durations result in better sound localization thresholds than short stimulus durations (Pollack & Rose 1967; Tollin et al. 2005). In birds, studies in owls did not find a difference in sound localization thresholds between closed-loop and open-loop conditions for frontal targets (Knudsen et al. 1979; Knudsen & Konishi 1979; Beitel 1991). In contrast, in Experiments I and II I will show that sound localization thresholds in starlings are better under closed-loop than under open-loop condition, and localization improves with head turns under closed-loop conditions. Head turns also represent a natural orienting response towards the sound, for example in birds and humans (e.g., Knudsen et al. 1979; Frost et al. 1989), in order to obtain visual information about the source (Heffner & Heffner 1992) that can improve stimulus source detection through audiovisual integration (e.g., Stein et al. 1989; Stein & Stanford 2008).

The stimulus spectrum represents another important factor influencing sound localization (for review, see Carlile et al. 2005). The full range of binaural and monaural cues is only provided if the stimulus comprises all frequencies within the hearing range of the subject. Consequently, localization thresholds for stimuli with broad spectra are superior to thresholds for stimuli with a limited frequency range, for example in

humans (e.g., Butler 1986) and cats (e.g., Martin & Webster 1987; Tollin et al. 2013). Some studies (Huang & May 1996; Martin & Webster 1987) even reported large difficulties of cats performing in sound localization tasks with pure tones, i.e. sounds of a single frequency. Similarly, sound localization thresholds in birds for broadband noise stimuli are better than or at least similar to thresholds for pure tones (e.g., Knudsen & Konishi 1979; Klump et al. 1986; Park & Dooling 1991), which is in line with results from *Experiments I* and *III* on the localization of static sounds in the European starling. Thus, only broadband noise stimuli that provide the full range of localization cues measure the best localization performance that an animal is capable of.

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### 3. METHODS IN SOUND LOCALIZATION: STATIC SOUNDS

Several major goals of behavioural sound localization studies require comparisons between sound localization thresholds measured in different studies and species. One of these goals is the identification of generalized principles that allow for predictions on sound localization mechanisms in other animals, including humans (e.g., Moss & Carr 2012). One example is the finding that sound localization thresholds can be predicted well by the width of the field of best vision in animals, but only poorly by their head size (Heffner 1997). Threshold comparisons between studies and species are also mandatory for finding correlations between sound localization thresholds and stimulus characteristics that provide an indication of the underlying processes. For example, the increase in human sound localization thresholds for pure tones at about 2 kHz has been connected to the inefficient utilization of the ITD and the IID in this frequency range (e.g., Mills 1958; Yost & Dye 1997). Another important goal requiring comparison of localization thresholds is the connection between behavioural results and neuronal responses. For example, Bala et al. (2003; 2007) showed in the barn owl (Tyto alba) that midbrain neuronal activity predicted behavioural sound localization thresholds.

A prerequisite for meaningful comparisons of sound localization thresholds is a similarity of the methods for determining thresholds across studies (e.g., Klump 2000). Signal detection theory (SDT; see Green & Swets 1966) provides the sensitivity measure d' that represents a unified framework for threshold criteria across different behavioural paradigms, and nearly all sound localization studies conform to similar threshold criteria. However, the characteristics of the experimental procedures in behavioural sound localization experiments are not unified across studies. Even most psychoacoustic textbooks do not discuss differences between methods (Letowski & Letowski 2012). In the following, I will review common paradigms for measuring the localization of static sound sources and discuss potential influences of differences in paradigms on resulting sound localization thresholds. Then, I will introduce the major goals and findings from Experiments I-III and provide an overview over the experimental paradigms and the results. A general discussion relates the findings to the differences between paradigms used in sound localization experiments. I will revise the traditional concept of classifying sound localization tasks and provide suggestions for a standardization of methods across studies measuring localization relative to other references.

### **3.1.** Absolute and relative types of task

In the generally accepted traditional concept, behavioural experiments on the localization of static sounds are classified as corresponding to one of two types of tasks (see Table 3.1): absolute and relative localization (e.g., Klump 2000; Moore et al. 2008; Moss & Carr 2012).

**Table 3.1:** Traditional classification of sound localization experiments into "absolute localization" and "relative localization". The absolute identification of the position of a single sound source measures precision and accuracy. The localization of the position of a sound source relative to the position of another sound source measures acuity and is often referred to as the minimum audible angle (MAA). The typical number of stimuli presented in each trial is often used to distinguish between the two types of sound localization task.

term	"absolute localization"	"relative localization"
type of task	absolute identification of sound source position	localization of sound source position relative to acoustic reference
measures	localization accuracy and precision	minimum audible angle (MAA) = localization acuity
typical number of stimuli in each trial	1	≥2

Studies on *absolute* sound localization correspond to the absolute identification of the position of a single sound source (Table 3.1). They often employ pointing or gazing towards the perceived position (e.g., Knudsen et al. 1979; Makous & Middlebrooks 1990; Carlile et al. 1997; Populin & Yin 1998; Spitzer & Takahashi 2006; Nodal et al. 2008; Moore et al. 2008; Ocklenburg et al. 2010; Tollin et al. 2013). Absolute sound localization tasks measure localization *accuracy* and *precision* (e.g., Heffner et al. 2005; Moore et al. 2008; Letowski & Letowski 2012). These two measures are illustrated in Figure 3.1. *Accuracy* describes a constant error in the response, for example due to unbalanced hearing environments (e.g., Letowski & Letowski 2012). In Figure 3.1, poor accuracy is represented by a constant localization error towards the right. *Precision* refers to a random error, for example due to internal noise (e.g., Letowski & Letowski 2012). Figure 3.1 illustrates that good precision corresponds to low variance in response direction. It is often defined as one standard deviation of the response direction (e.g., Letowski & Letowski 2012).



**Figure 3.1**: The concepts of accuracy and precision illustrated by a simulated game of darts (modified after Heffner et al. 2005). Circles represent the dartboard, crosses show locations of dart throws. Accuracy describes a constant error in location to one side. In this example, poor accuracy is represented by a constant error to the right. Precision represents the variance in locations, poor precision corresponds to large variance.

The traditional concept of *relative* localization corresponds to the localization of a sound source relative to another sound source position that represents an acoustic reference (Table 3.1) and measures how well sound source positions can be discriminated (e.g., Mills 1958; Perrott & Pacheco 1989; Perrott & Saberi 1990; Bala et al. 2003; Grantham et al. 2003; Spitzer et al. 2003; Macaulay et al. 2010). Thresholds are defined as the minimum audible angle (MAA), or localization *acuity* (e.g., Heffner et al. 2005; Moore et al. 2008). Figure 3.2 illustrates that acuity is often compared to the precision component measured in absolute tasks. This is based on the assumption that the variance in the internal spatial representation of single sounds affects the discriminability of the internal spatial representation of two sounds (e.g., Makous & Middlebrooks 1990; Recanzone et al. 1998).

a) Good Precision → Good Acuity
b) Poor Precision → Poor Acuity
the precision → food Acuity
the precision → Poor Acuity
the precision →

**Figure 3.2:** Concept of the influence of precision on acuity (modified after Heffner et al. 2005). Red and blue circles represent the positions of two sound sources. Acuity measures how well the two sound sources can be discriminated, and this depends on the internal spatial representation of each target. a) Good precision for each sound source indicates precise internal spatial representations of each target. This results in good discriminability of the internal spatial representations, so that acuity is good. b) Poor precision for each sound source indicates that their internal spatial representations are broad. This results in an overlap of the internal spatial representations of the two sound sources. The discriminability of these internal spatial representations of the two sound sources. The

Much experimental evidence confirms the assumption that the spatial discrimination of sound sources (i.e. acuity) depends on the variance in the internal spatial representation of single sound sources (i.e. precision). In humans, precision and acuity depend on similar stimulus characteristics. For example, both decrease with stimulus laterality (e.g., Makous & Middlebrooks 1990; Freigang et al. 2014; but see Recanzone et al. 1998) and age (Freigang et al. 2014), and both measures are better for broadband noise that provides the full range of localization cues than for pure tones (e.g., Recanzone et al. 1998). Also, precision develops with age similarly to acuity (Kühnle et al. 2013). On the other hand, some studies suggest that the processing underlying precision deviates from the processing underlying acuity. In barn owls, precision is similar in azimuth and elevation for frontal regions (Knudsen et al. 1979), but acuity differs between azimuth and elevation (Bala et al. 2007). In the same species, simulated reflections decrease acuity (Spitzer et al. 2003) but not precision (Spitzer & Takahashi 2006). In cats, lesions in dorsal and intermediate acoustic striae that connect the dorsal CN with the auditory brainstem and midbrain result in poorer precision but do not affect acuity (May 2000).

In humans, precision reaches about 3° for frontal positions (e.g., Makous & Middlebrooks 1990; Carlile et al. 1997), while acuity can reach about 1° (e.g., Mills 1958; Perrott 1969; Perrott & Pacheco 1989; Perrott & Saberi 1990). In cats and owls,

precision and acuity reported in multiple studies suggest that precision is superior to acuity (Moore et al. 2008). However, the comparison of absolute values of precision and acuity is complicated. The methods in absolute tasks that measure precision differ from the methods in tasks on localization relative to another sound source that measure acuity. For example, absolute localization often involves motor responses like gaze orientation or pointing (e.g., Knudsen et al. 1979; Carlile et al. 1997; for review, see Letowski & Letowski 2012), so localization responses can be biased by motor errors (e.g., Brown 1995; Moore et al. 2008). Relative localization, on the other hand, is based on perceptual tasks (e.g., Mills 1958; Bala et al. 2003). The comparison of absolute values of precision with absolute values of acuity is complicated further by the fact that even within the two types of task, experimental procedures significantly differ between studies, which may affect reported thresholds. These differences within absolute and relative types of task are discussed in the following sections. The most meaningful comparisons of absolute values of precision and acuity stem from two studies (Recanzone et al. 1998; May 2000) reporting both measures for the same individuals and for broadband noise presented from the front of the subjects. This represents the most basic stimulus type, since it provides the full range of localization cues in the frontal region where localization is best. Human participants in the study by Recanzone et al. (1998) reached a precision of 4-6° and an acuity of about 3° for this stimulus type. In the study by May (2000), cats localized this stimulus type with a precision of 6-9° and an acuity of less than 6° (the smallest angular separation of sound sources tested in that study). Results from these two studies suggest that acuity is superior to precision both in humans and in cats.

Thus, the correspondence between sound localization thresholds measured in absolute and relative types of task remains ambiguous. Most studies comparing sound localization thresholds distinguish between these two types of task and only compare thresholds within each type of task (e.g., Heffner 1997; Klump 2000; Moss & Carr 2012). However, this is based on the often unexpressed assumption that within each type of task, the characteristics of the experimental procedures do not affect sound localization thresholds. In the following, I will introduce mostly unexpressed differences between paradigms that may affect thresholds and thus the significance of threshold comparisons.

# 3.1.1. Differences within procedures traditionally classified as absolute tasks

Experiments measuring absolute localization employ action paradigms or categorical paradigms. In the following, I will shortly discuss how the methods in these paradigms may affect results. Afterwards, I will focus on the effect of methods in a specific type of categorical paradigm often used in animal sound localization research.

#### Action and categorical paradigms

Most experiments on absolute sound localization measure the absolute identification of a single sound source position through motor actions, for example through head pointing (e.g., Knudsen et al. 1979; Carlile et al. 1997). As outlined above, motor errors can bias responses measured in this paradigm (for review, see Letowski & Letowski 2012). Results should report accuracy as well as precision (e.g., Makous & Middlebrooks 1990; Carlile et al. 1997; Ocklenburg et al. 2010), but many studies merge these two measures and report a single error value (see Letowski & Letowski 2012) which complicates the comparison of results across studies. Action paradigms allow to minimize the influence of sound localization cues from other modalities, for example by conducting experiments in total darkness (e.g., Carlile et al. 1997).

Other studies on absolute sound localization require subjects to categorize the sound source (e.g., Jenkins & Masterton 1982; Musicant & Butler 1984; Abel et al. 2000; Malhotra et al. 2004; Nodal et al. 2008; Grieco-Calub & Litovsky 2010; Macaulay et al. 2010). For example, Macaulay et al. (2010) numbered the loudspeakers and subjects reported the number of the loudspeaker presenting the stimulus. This procedure measures the absolute identification of the sound source position. However, visual cues guide the subject's responses: the subject indicates the visually determined category that is closest to the perceived position of the auditory stimulus. Thus, unlike many action paradigms, absolute tasks requiring categorization are influenced by cues from other modalities. If the number of categories is sufficiently high (e.g., a semicircle of loudspeakers each separated by 15°), precision and accuracy can be calculated from categorical responses (Letowski & Letowski 2012).

### Direction discrimination paradigm with a single stimulus

Studies on sound localization in animals often employ a specific type of categorical paradigm (illustrated in Figure 3.3): left/right discrimination paradigms that present a single stimulus in each trial and require subjects to respond to the side at which the stimulus was presented (e.g., Casseday & Neff 1973; Terhune 1974; Casseday & Neff 1975; Gatehouse & Shelton 1978; Heffner & Masterton 1980; Heffner & Heffner 1982;

Heffner & Heffner 1984; Klump et al. 1986; Heffner & Heffner 1988a; Heffner & Heffner 1988b; Park & Dooling 1991; Heffner & Heffner 1992; Parsons et al. 1999; Nelson & Suthers 2004; Maier & Klump 2006; Bodson et al. 2006; Carney et al. 2011). This paradigm is also often used in research on sound localization in hearing-impaired children (e.g., Litovsky et al. 2006; Beijen et al. 2010; Godar & Litovsky 2010; Grieco-Calub & Litovsky 2010). With a single stimulus in each trial, these experiments are classified traditionally as absolute tasks (see Table 3.1).



**Figure 3.3:** Example for the procedure in a left/right discrimination experiment with a single stimulus. When the subject is at a waiting position (a), a single stimulus is presented from one of the sound sources (b). The subject reports the perceived side of the stimulus (left or right) by moving to one of two response positions (c) corresponding to the side of stimulus presentation.

Results from left/right discrimination paradigms with a single stimulus correspond to absolute measures of sound localization only if the subjects identify the absolute position of the single sound source. This may be the case if the stimuli are presented from one pair of visible sound sources (e.g., Klump et al. 1986): with a directional response to one side, the subject may indicate the identification of the sound source presenting the stimulus and therefore its absolute position (Figure 3.4a). However, if the sound sources are invisible (Figure 3.4b), subjects lack visual information about absolute sound source positions (e.g., Gatehouse & Shelton 1978). In these cases, subjects need to decide whether the sound source was located to the left or to the right of a non-acoustic spatial frame of reference, for example at 0° azimuth (Figure 3.4b). Thus, left/right discrimination paradigms with single stimuli presented from invisible sound sources represent a type of relative task: the localization task does not correspond to the traditional classification of a relative localization task that measures

localization relative to an acoustic reference (Table 3.1). Rather, it represents a second type of relative task that is not included in this traditional classification. *Experiment III* is the first study to introduce this type of task.



**Figure 3.4:** Left/right discrimination experiments with a single stimulus can represent an absolute localization task or a localization task relative to a non-acoustic reference. Relating responses to angular separations differs between the corresponding analyses. a) When stimuli are presented from one pair of visible sound sources, the type of task may be absolute. The subject has visual information about the position of the two sound sources. It may discriminate which of the two sound sources presented a single stimulus. The left/right response therefore may indicate the absolute position of the stimulus. Since the subject discriminates between the two sound source positions, the analysis relates responses to the angular separation of the pair of sound sources. b) If the subject lacks visual information about the position of the sound sources, for example due to an opaque cloth in front of the sound sources as indicated by the curved dashed line, the type of task is relative. When a stimulus is presented, the subject needs to compare the perceived sound source position to another spatial frame of reference to decide whether it was presented from the left or from the right. This frame of reference can be at 0° azimuth, as indicated by the vertical dashed line. Therefore, the subject localizes sound relative to a non-acoustic reference. The analysis for this type of task relates responses to the angular separation of the sound sources to 0°.

Thus, left/right discrimination experiments with single stimuli correspond either to absolute localization or to localization relative to a non-acoustic reference. This has broad implications for analysing responses in this paradigm. If the type of task corresponds to absolute localization, subjects discriminate between the absolute positions of the two sound sources. In this case, responses are analysed in relation to the angular separation of the pair of sound sources, as illustrated in Figure 3.4a (e.g., Park & Dooling 1991). If the type of task corresponds to localization relative to a non-acoustic reference position, responses are analysed in relation to the angular separation of each sound source to 0°, as illustrated in Figure 3.4b (e.g., Bodson et al.
2006; see Keating et al. 2013). *Experiment III* shows that since the angular separation of a pair of sound sources is twice as large as the angular separation of the individual sound source positions to 0°, sound localization thresholds differ at least by a factor of 2 between the two analysis methods. As pointed out in *Experiment III*, this difference between calculated thresholds can be further increased by directional response bias, i.e. the tendency to respond to one side more often than to the other side. If studies choose the analysis method that does not correspond to the type of task (e.g., Gatehouse & Shelton 1978; Heffner & Heffner 1984; Maier & Klump 2006), comparisons of thresholds to other studies are complicated.

# 3.1.2. DIFFERENCES WITHIN PROCEDURES TRADITIONALLY CLASSIFIED AS RELATIVE TASKS

Sound localization studies on acuity are traditionally classified as relative types of task, i.e. localization relative to an acoustic reference (see Table 3.1). Besides operant conditioning methods (e.g., Heffner & Heffner 1982; Heffner & Heffner 1984), studies on acuity employed conditioned avoidance (e.g., Heffner et al. 1994; Heffner et al. 2001; see Heffner & Heffner 1995), pupillary dilation response (e.g., Bala & Takahashi 2000; Bala et al. 2003) or heart-rate conditioning (e.g., Lewald 1987). Conditioned avoidance results in thresholds similar to behavioural measures (Heffner & Heffner 1988a), and the pupillary dilation response correlates well with the spatial resolving power of neurons (Bala et al. 2007). However, criteria used in heart-rate conditioning differ considerably from psychophysical criteria. For example, only one increase in the heart beat rate would have been sufficient to improve sound localization thresholds in the study by Lewald (1987). This complicates quantitative comparisons of results from heart-rate conditioning to results from studies using the other procedures (Klump 1995).

Experiments measuring acuity provide reference sounds and employ either a direction discrimination paradigm or a difference detection paradigm. In the following, I will discuss how these paradigms may affect results.

#### Direction discrimination paradigm with reference sounds

Some sound localization studies measuring acuity require subjects to identify whether a test stimulus position was to the left or to the right of a standard stimulus position, as illustrated in Figure 3.5 (e.g., Mills 1958; Perrott 1969; Renaud & Popper 1975; Perrott & Pacheco 1989; Perrott & Saberi 1990; Litovsky & Macmillan 1994; Grantham et al. 2003; Macaulay et al. 2010; Croghan & Grantham 2010). These studies often present the standard stimulus from a position known to the subject, for example from

0°, as illustrated in Figure 3.5. Under these conditions, subjects can ignore the standard stimulus and base responses only on the direction of the single test stimulus, which would correspond to a left/right discrimination paradigm with a single stimulus that is traditionally classified as an absolute task (compare Figure 3.3 and Figure 3.5). Ignoring the standard stimulus in this paradigm improves performance and therefore may lead to an overestimation of acuity (Hartmann & Rakerd 1989; Litovsky & Macmillan 1994).



**Figure 3.5:** Example for a relative localization experiment with a direction discrimination paradigm. Typically, a single standard stimulus from one azimuthal position is followed by a test stimulus from another azimuthal position. The subject reports the perceived position of the test stimulus relative to the standard stimulus (i.e., left or right of the standard stimulus) by approaching one of two response positions.

#### Difference detection paradigm

Many studies on acuity employ a difference detection paradigm that measures how well subjects can detect a difference between two sound source positions (illustrated in Figure 3.6). The direction of the switch in position is either predictable (e.g., Brown et al. 1978; Heffner & Heffner 1985; Heffner & Heffner 1987; Martin & Webster 1987; Heffner & Heffner 1988a; Heffner & Heffner 1988c; Heffner & Heffner 1989; Heffner & Heffner 1983; Heffner et al. 1994; Heffner et al. 1999; Heffner et al. 2001; Spitzer et al. 2003) or unpredictable (e.g., Lewald 1987; Huang & May 1996b; Recanzone et al. 1998; Bala & Takahashi 2000; May 2000; Bala et al. 2003). Cues predictive of target position can improve auditory spatial discrimination in humans, which suggests that spatial attention can improve localization (Sach et al. 2000; Spence & Driver 1994). This may result in better sound localization thresholds in paradigms with predictable directions of switch in position.



**Figure 3.6:** Example for a relative localization experiment with a difference detection paradigm. A standard stimulus is presented from one azimuthal position and typically repeated (three times in this example). Then, a test stimulus from another azimuthal position replaces the standard stimulus. The subject is trained to report the detection of the difference in sound source position by leaving the waiting position.

The cognitive load in a difference detection paradigm (Figure 3.6) is lower than the discrimination of two alternatives in a direction discrimination paradigm (Figure 3.5) that requires stimulus classification (e.g., Lit 2009; Walker et al. 2009). This may lead to diverging thresholds between difference detection and direction discrimination paradigms in animals with limited cognitive processing. However, the difference in change in cerebral blood flow in the right parietal cortex of humans during sound localization is small between difference detection and direction discrimination tasks (Zatorre et al. 2002).

An important factor that may influence results from paradigms measuring acuity is the presentation of more than one standard stimulus. *All* of the studies cited above that employed a direction discrimination paradigm (Figure 3.5) presented only a single standard stimulus prior to the test stimulus. However, *all* of the studies cited above that employed a difference detection paradigm (Figure 3.6) employed multiple repetitions of the standard stimulus before a test stimulus was presented. It is possible that a repeated presentation of a stimulus may reduce the standard deviation of its internal spatial representation, which may result in better localization acuity (Figure 3.2). For example, the ITD tuning of neurons in barn owl nucleus laminaris improves with an increase in the number of stimulus repetitions and converges after about 6 stimulus presentations (Christianson & Peña 2006). In *Experiment 1*, I will present a study on acuity in starlings that employs a difference detection paradigm (see Figure 3.6) with a varying number of standard stimulus presentations. I will show that thresholds improved with an increase in the number of standard stimulus presentations.

suggests that the number of stimulus repetitions affected acuity reported in studies with a difference detection paradigm.

Thresholds measured in a difference detection paradigm may also be affected by an ongoing presentation of the standard stimulus during the response interval after test stimulus presentation (e.g., Brown et al. 1978; Huang & May 1996b; May 2000). In these studies, each trial comprises more than one switch in stimulus position, which may increase the probability of detecting a switch in stimulus position and therefore improve acuity.

# 3.2. MAJOR GOALS

The first part of this dissertation focuses on the role of methods on sound localization thresholds and establishes the European starling as an animal model for sound localization research.

*Experiment I* measured acuity in the European starling with stimuli that determined the effect of stimulus spectrum and duration on sound localization processing in this species. One major goal was to determine whether standard stimulus repetitions that are common in the difference detection paradigm (Figure 3.6) affect acuity.

Based on a superior acuity under closed-loop compared with open-loop conditions in starlings shown in *Experiment I, Experiment II* analysed whether starlings used head turns during closed-loop stimulus presentation as a strategy to improve sound localization. An increase in acuity with head turns in the starling would show that sound localization in birds can benefit from head turns, which would agree with similar effects in human sound localization.

The major goal of *Experiment III* was to introduce a localization task relative to a nonacoustic reference (Figure 3.4b) that is not covered in the traditional classification of localization experiments shown in Table 3.1. The study provides a guideline when left/right discrimination experiments with a single stimulus represent an absolute localization task or a localization task relative to a non-acoustic reference. Another goal was to quantify how the implications of the analysis methods for these two types of task affect calculated thresholds.

# **3.3.** Experimental paradigms

In the behavioural experiments on sound localization in starlings, all sound sources were shielded from the birds' view by an acoustically transparent but optically opaque cloth (see Figure 3.7) to minimize expectation of stimulus position.



**Figure 3.7:** Photographs of the setup for the experiment on localization acuity in the starling. An optically opaque cloth shielded the loudspeakers from the starlings' view. a) View of the experimental cage through the door of the double-walled sound attenuating chamber. b) Stimuli were presented through a semicircle of loudspeakers. c) Top view of the experimental cage with the optically opaque cloth shielding the loudspeakers from view.



**Figure 3.8:** Frames in videos recorded from top view during *Experiment I* and *Experiment III.* a) Video frame from *Experiment I* on localization acuity in the starlings. A repeated standard stimulus from one position was replaced by a test stimulus from another position, and the bird was trained to report switches in stimulus position by leaving the waiting position (see Figure 3.6). The direction of the beak is tagged green to illustrate the analysis of head directions in *Experiment II.* b) Video frame from *Experiment III* on localization relative to a non-acoustic reference. Birds were trained to detect the side where a single stimulus was presented from by moving to the left or the right response position (see Figure 3.3). For a better contrast of the starling from the background in the video recordings in *Experiment III*, yellow foam provided a consistent background.

*Experiment 1* measured sound localization acuity in the European starling. In the operant Go/NoGo procedure the standard stimulus consisted of sounds from a single position which was repeated up to five times and then replaced by the test stimulus with identical properties from another azimuthal position. Starlings were trained to detect switches in stimulus position by leaving the waiting position (see Figure 3.6 and Figure 3.8a). Angular separations between repeated standard stimuli and test stimuli varied between 13° and 90°. The direction of switch in stimulus position was

unpredictable to the birds, and the standard stimulus position varied between trials in order to minimize attention to expected stimulus positions. Stimulus types comprised open-loop broadband noise as well as pure tones between 1 and 4 kHz, and closed-loop broadband noise and 2 kHz tones.

*Experiment II* analysed the benefit of head turns on acuity in the European starling. *Experiment I* recorded the starlings during the experiments on video from top view at a rate of 15 frames per second. In *Experiment II*, the direction of the starling bill was tagged (see Figure 3.8a) in specific frames. For open-loop stimuli with a duration of 0.1 s, these comprised the last frame before the start of the stimulus, all two to three frames during the presentation of the stimulus, and the first frame after the stimulus terminated. For closed-loop stimuli with a duration of 1 s, the head direction in the fourth, fifth, sixth and tenth frame was also tagged, thereby making sure to detect every movement of the head. Comparisons of head turns during the presentation of the stimulus. The number of head turns was grouped 0-1, 1-2 and 2 or more head turns per stimulus presentation in order to enable the calculation of acuity for each group.

*Experiment III* measured sound localization in the European starling with a task that may be solved by localization relative to a non-acoustic reference. In a two-alternative forced choice procedure, a single stimulus was presented in each trial, and starlings were trained to give a directional response to the side where the stimulus was presented at (see Figure 3.3 and Figure 3.8b)). Sound source positions ranged between 0° and ±51° azimuth. Stimulus types comprised broadband noise as well as pure tones between 1 and 4 kHz presented under open-loop conditions. Since sound sources were invisible to the starlings (Figure 3.7), directional responses were based on comparisons of perceived sound source position to a non-acoustic spatial frame of reference such as the position at 0° azimuth.

# **3.4.** Summary of the results

*Experiment 1* measured sound localization acuity in the European starling, i.e. localization relative to an acoustic reference. The birds reached an acuity of 17° for closed-loop broadband noise and 29° for open-loop broadband noise. Acuity for closed-loop pure tones linearly improved from 26° to 19° for an increase in frequency from 1 to 4 kHz. Acuity increased with the number of standard stimulus presentations. For example, the mean sensitivity d' for closed-loop 4 kHz tones with an angular separation of 26° increased from 0.55 for one standard stimulus to 1.72 for five standard stimuli. The tendency to respond although no switch in stimulus position was presented did not increase with an increase in the number of standard stimulus

presentations, so a change in response tendency cannot explain the increase in acuity with standard stimulus repetitions. Acuity did not differ between four and five standard stimulus presentations that represented the highest numbers of standard stimuli included in the experiment.

*Experiment II* analysed the effect of head turns on sound localization acuity in the European starling based on video recordings from *Experiment I*. The mean number of head turns per stimulus presentation reached 1.7 for closed-loop and 0.6 for open-loop stimuli, which indicates that the starlings used closed-loop stimuli to make more head turns during stimulus presentation compared to open-loop stimuli. For closed-loop stimuli, the mean sensitivity d' reached 1.2 for 0-1 head movements per stimulus presentation, which was lower than a mean sensitivity d' of 2.2 and 1.8 for 1-2 and 2 or more head movements per stimulus presentation, respectively. This shows that head turns improved acuity in the starlings.

Experiment III measured sound localization relative to a non-acoustic reference in the European starling. The experiment introduces this type of task that does not correspond to either of the two types of task in the traditional classification of sound localization studies (Table 3.1). Thresholds were lower than acuity in the starling measured in Experiment I, reaching 8° to 12°. This indicates that the internal spatial representation of the modality used as a reference was more precise than the internal spatial representation of a sound source. The study also shows that thresholds calculated in left/right discrimination paradigms with a single stimulus depend on the method for analysing results. When responses are related to the angular separation of sound source pairs (which is the analysis method corresponding to an absolute localization task, see Figure 3.4a), thresholds are poorer than when responses are related to the angular separation of each sound source to 0° (which is the analysis method corresponding to a localization task relative to a non-acoustic reference like in Experiment III, see Figure 3.4b). Experimental results and simulated responses showed that besides the difference in relating responses to azimuthal angle, this difference results from potential directional response bias. This bias increases thresholds calculated with the analysis method corresponding to an absolute localization task, whereas thresholds calculated with the analysis method corresponding to a localization task relative to a non-acoustic reference accounts for this bias.

#### 3.5. GENERAL DISCUSSION

*Experiments I-III* establish the European starling as an animal model for the processes underlying sound localization by measuring two types of relative localization, acuity and localization relative to a non-acoustic reference, and investigating the effect of head turns on acuity. The results demonstrate that the European starling is well-suited as an animal model for sound localization. Similar to humans, acuity is superior under closed-loop compared to open-loop conditions, and head turns during the presentation of closed-loop stimuli improve localization. Moreover, acuity for broadband noise is at least equal to acuity for pure tones, although the results do not show a clear benefit of the full range of localization cues. Thresholds further relate well to the physical interaural cues determined by Klump and Larsen (1992), and the improvement in sound localization thresholds with an increase in frequency from 1 to 4 kHz as well as the orienting towards a sound source corresponds well to findings in other birds (e.g., Knudsen et al. 1979; Park & Dooling 1991).

In the following, I will relate the results from Experiments I and III to the differences in methods that are used to study sound localization introduced in Chapter 3.1. I will discuss how the influence of standard stimulus repetitions on acuity in the starling shown in *Experiment I* affects the comparability of thresholds measured in paradigms that include standard stimulus repetitions. Based on *Experiment III* and Chapter 3.1, I will then revise the traditional classification of sound localization tasks. Finally, I will suggest standards for stimulus types, procedures and analyses employed in experiments on sound localization relative to an acoustic or to a non-acoustic reference that would improve comparability of reported thresholds across future studies.

# 3.5.1. INFLUENCE OF STANDARD STIMULUS REPETITIONS ON LOCALIZATION THRESHOLDS

*Experiment I* showed that acuity in the starlings increases with the number of standard stimulus presentations preceding the test stimulus. In the following, I will discuss the important implications for interpreting results on acuity from previous studies.

#### Acuity measured with single and multiple standard stimuli

Sound localization experiments that measure acuity employ tasks that require localization relative to an acoustic reference, the standard stimulus. Studies that employing a direction discrimination paradigm (Figure 3.5) typically present a single standard stimulus (e.g., Perrott & Saberi 1990; Perrott & Pacheco 1989; Macaulay et al. 2010; Mills 1958; Croghan & Grantham 2010; Renaud & Popper 1975; Perrott 1969; Grantham et al. 2003; Litovsky & Macmillan 1994). However, studies employing a difference detection paradigm (Figure 3.6) typically present multiple standard stimuli (e.g., Brown et al. 1978; Heffner & Heffner 1985; Heffner & Heffner 1987; Martin & Webster 1987; Lewald 1987; Heffner & Heffner 1983; Heffner et al. 1994; Huang & May

1996a; Recanzone et al. 1998; Heffner et al. 1999; Bala & Takahashi 2000; May 2000; Heffner et al. 2001; Bala et al. 2003; Spitzer et al. 2003). The profound improvement of acuity with an increase in the number of standard stimulus presentations in *Experiment I* predicts better acuity in previous studies employing multiple standard stimuli compared to studies employing a single standard stimulus.

Comparisons of acuity reported in studies with one standard stimulus to acuity reported in studies with multiple standard stimuli are complicated by the fact that only studies in the same species allow for meaningful comparisons. From all the studies cited above, humans represent the only species that participated in experiments measuring acuity with one standard stimulus (e.g., Mills 1958; Perrott & Saberi 1990) and with multiple standard stimuli (Recanzone et al. 1998). As outlined in Chapter 3.1.2, comparisons between these studies are complicated since studies on acuity with one standard stimulus employed a direction discrimination paradigm that may overestimate acuity: subjects could ignore the standard stimulus (compare Figure 3.3 and Figure 3.5), a strategy that improves acuity in humans (Hartmann & Rakerd 1989; Litovsky & Macmillan 1994). This does not allow for meaningful comparisons of absolute acuity values reported in previous studies with paradigms employing a single standard stimulus or multiple standard stimulus presentations.

#### Variance in acuity measured with multiple standard stimuli

In Experiment I, acuity did not differ between four and five standard stimulus presentations. This suggests an asymptotic function of the influence of the number of standard stimuli on acuity that increases especially for the first few standard stimulus presentations. In line with this finding, the ITD tuning in the nucleus laminaris of barn owls converges after about six stimulus presentations (Christianson & Peña 2006). In some studies on acuity with multiple standard stimuli, only large numbers of standard stimuli were presented (e.g., Spitzer et al. 2003: 39 standard stimuli in each trial). In other studies, low numbers of standard stimuli like one or two were presented in some trials (Brown et al. 1978; Heffner & Heffner 1985; Heffner & Heffner 1987; Heffner & Heffner 1988a; Heffner & Heffner 1988c; Heffner & Heffner 1989; Heffner & Heffner 1993; Heffner et al. 1994; Recanzone et al. 1998; Heffner et al. 1999; Heffner et al. 2001). An effect of the number of standard stimuli similar to Experiment I would have resulted in a difference in the variance in the individual subjects' responses between these two types of studies. In studies that only presented large numbers of standard stimuli, the effect of standard stimulus repetitions on the probability of detecting a switch in stimulus position would have been similar between different numbers of standard stimuli. For example, Experiment I predicts that acuity measured with 30 standard stimuli is likely to be similar to acuity measured with 35 standard stimuli. Compared to these studies, the variance in the individual subjects' probability of detecting a switch in stimulus position would have been larger in studies that included low numbers of standard stimuli in some trials. For example, *Experiment I* predicts that acuity measured with 1 standard stimulus may be poorer than acuity measured with 5 standard stimuli.

Meaningful comparisons of the variance in the subjects' responses under these two conditions in the literature require that acuity was measured in the same species. From all the studies cited above that measured acuity with multiple standard stimuli, the cat is the only species that participated in studies that included low numbers of standard stimuli in some trials (Heffner & Heffner 1988a: 0-9 standard stimuli in each trial) or only large numbers of standard stimuli (Huang & May 1996b: 5-10 standard stimuli in each trial; May 2000: 20-40 standard stimuli in each trial). However, in these studies in the cat, only the mean acuity was reported for each subject, but not the individual variance in responses. This does not allow for comparisons between the variances in the individual subjects' responses measured under these two conditions.

#### Comparison of acuity and precision measured in previous studies

As outlined in Chapter 3.1 and illustrated in Figure 3.2, acuity is assumed to depend on precision. The most meaningful comparison of these two measures stems from a study in humans (Recanzone et al. 1998) and a study in cats (May 2000) that measured precision as well as acuity in the same individuals, under similar experimental conditions and with the same stimulus types. For the most basic stimulus characteristics, broadband noise presented from the front of the subjects, acuity was superior to precision in both studies. However, the effect of the number of standard stimulus presentations on acuity shown in *Experiment I* suggests that acuity in these two studies may have been influenced by repetitions of the standard stimulus. In both studies, a difference detection paradigm was used to present a standard stimulus multiple times (Recanzone et al. 1998: 2-6 standard stimuli in each trial; May 2000: 20-40 standard stimuli in each trial), and then a sound source from another azimuthal position was activated. An improvement in acuity with an increase in standard stimulus repetitions, as demonstrated in *Experiment I*, may explain the difference between precision and acuity reported by Recanzone et al. (1998) and May (2000). This complicates comparisons of precision and acuity measured in these two studies.

Studies on acuity employ either a direction discrimination paradigm or a difference detection paradigm. As outlined above, both paradigms may overestimate this measure. In studies employing a direction discrimination paradigm with a standard stimulus at a predictable position, subjects can ignore the standard stimulus to improve performance (Hartmann & Rakerd 1989; Litovsky & Macmillan 1994), as discussed in Chapter 3.1.2. In studies employing a difference detection paradigm, acuity may have improved with multiple standard stimuli, as predicted by results from

*Experiment I.* Acuity unbiased by the number of standard stimuli would correspond to similar internal distributions of standard and test stimulus position, i.e. acuity measured with only one standard stimulus preceding the test stimulus. Thus, previous studies may not allow for meaningful comparisons of absolute values of acuity and precision.

#### 3.5.2. REVISION OF THE TRADITIONAL CONCEPT OF SOUND LOCALIZATION TASKS

Traditionally, studies on sound localization are classified as either absolute or relative localization (see Table 3.1). Absolute localization refers to the absolute identification of sound source position. As discussed in Chapter 3.1.1, absolute tasks employing action paradigms can minimize the influence of other modalities, for example if experiments are carried out in total darkness (e.g., Carlile et al. 1997). In contrast, absolute tasks employing categorical paradigms are influenced by other modalities. For example, subjects can report the visually identified loudspeaker number that is closest to auditory perception of sound source position. Thus, absolute localization should be divided by the influence of other modalities on responses in the revised classification of sound localization tasks shown in Table 3.2.

Relative localization traditionally refers to localization relative to an acoustic reference, for example the detection of a difference in two sound source positions (e.g., *Experiment I*; Bala et al. 2003). *Experiment III* introduced a second type of relative localization task: localization relative to a non-acoustic reference. Thus, the traditional term "relative localization" becomes ambiguous in the revised classification of sound localization tasks shown in Table 3.2. The term "relative localization" should not be used without specifying whether the type of task requires localization relative to an acoustic reference.

**Table 3.2:** Revised classification of sound localization tasks. The traditional classification shown in Table 3.1 only distinguishes between absolute and relative studies. The revised classification shows that absolute localization tasks should be distinguished by the influence of other modalities on responses. Also, relative localization tasks should be distinguished between acoustic and non-acoustic references. Three of the four types of task in the revised classification typically present one stimulus in each trial, so this number should not be used to classify the type of localization task.

term	"absolute lo	ocalization"	"relative localization"	
type of task	absolute identification of sound source position <u>without</u> influence from other modalities	absolute identification of sound source position <u>with</u> influence from other modalities	localization of sound source position relative to <u>acoustic</u> reference	localization of sound source position relative to <u>non-acoustic</u> reference
typical number of stimuli in each trial	1	1	≥2	1

In the traditional concept, the number of stimulus presentations in each trial indicates the type of sound localization task (e.g., Klump 2000; Moss & Carr 2012): one stimulus per trial would indicate an absolute type of task, multiple stimuli per trial would indicate a relative type of task (see Table 3.1). However, the introduction of the localization task relative to a non-acoustic reference in *Experiment III* implies that the number of stimuli in each trial is in fact a poor indicator of the type of task. While tasks on localization relative to an acoustic reference present multiple stimuli per trial, tasks on localization relative to a non-acoustic reference like in *Experiment III* typically present a single stimulus in each trial. Thus, experiments with a single stimulus can represent a relative task, and correspondingly the single stimulus per trial is not a unique feature of absolute types of task. Therefore, the number of stimuli presented in each trial should not be used to classify the type of sound localization task.

#### 3.5.3. Suggestion for standardized procedures in relative types of task

As outlined in this general discussion and in Chapter 3.1, the large number of procedures and stimulus types that are used to study sound localization often results in poor comparability of results across studies. Furthermore, it is not surprising that they often lead to confusion of measures. For example, some studies (e.g., Terhune 1974; Park & Dooling 1991; Parsons et al. 1999; Litovsky et al. 2006; Bodson et al. 2006; Grieco-Calub & Litovsky 2010; Godar & Litovsky 2010; Beijen et al. 2010) and auditory textbooks (e.g., Moss & Carr 2012) mislabel left/right discrimination paradigms with a single sound as MAA thresholds, i.e. acuity, instead of the traditional

classification as absolute thresholds (see Table 3.1). Similarly, measurements of acuity may be mislabelled as an absolute threshold (e.g., Lewald 1987). Also, Mills (1958) introduced the MAA as "the smallest detectable difference between the azimuths of identical sources of sound" (Mills 1958, p.237), but instead of employing a difference detection paradigm (see Figure 3.6), his experiment employed a direction discrimination paradigm (see Figure 3.5). Probably due to this mixture of methods and definitions, these two paradigms are often treated interchangeably despite their potential difference in cognitive load and sensory performance measured (see Chapter 3.1.2).

Standardized procedures would improve the possibility to compare thresholds across studies and reduce the confusion of measures. Especially studies on relative types of task show large differences between procedures (see Chapter 3.1.2), and these differences are even further increased by the introduction of another type of relative task in *Experiment III*. Based on potential influences of differences in methods on thresholds, as discussed in Chapter 3.1 and *Experiments I* and *III*, the following sections provide suggestions for standards in relative types of task.

# Suggestion for standards in experiments on localization relative to an acoustic reference

In the revised classification of sound localization tasks (see Chapter 3.5.2), one of the two types of relative tasks is the localization of sounds relative to an acoustic reference. The standards suggested for this type of task are listed in Table 3.3. *Experiment I*, which measured acuity in the European starling, conformed to all of the suggested standards for this type of task.

**Table 3.3:** Suggestion for standards in experiments on localization relative to an acoustic reference. The colours represent suggestions for standards in the stimulus presentation (blue), the procedure (green) and the analysis (red). For details, see text.

	Stimuli		
Suggestion for standard	Procedure	Rationale	
	Analysis		
Shield sound sources from view		Unpredictable stimulus position	
Include broadband noise		Measures best localization performance subject is capable of	
Include tones, e.g. between 1 and	4 kHz	Measures influence of ITD and IID on localization	
Present changes in position in bo with equal probability	th directions	Unpredictable stimulus position	
Vary positions of standard and te	st stimuli	Unpredictable stimulus position	
Single test stimulus		Predictable variance of internal representation of test stimulus	
No standard stimulus after test st	imulus	Avoids multiple changes in stimulus position	
Response interval ≤ stimulus repe	etition rate	Avoids absence of stimulus as cue	
No left/right discrimination		Lower cognitive demands	
		Avoids ignoring the standard stimulus	
Relate responses to angular separation of sound sources		Corresponds to task: Detection of difference in sound source positions	
Threshold criterion d'=1.0 or equal		Comparable thresholds across studies	
Measure effect of standard stimulus repetitions		Standard stimulus repetitions may improve acuity	
Include results for the acuity for 1 standard stimulus presentation		Allows for comparisons to precision in absolute types of task	

Experiments with this type of task should shield sound sources from view to decrease the possibility of predicting the stimulus position or the direction of switch in stimulus position. Stimulus types should include broadband noise to measure localization with the full range of binaural and monaural cues, i.e. the best localization the subject is capable of. Pure tones (e.g. between 1 and 4 kHz) allow to measure the influence of ITD and IID on sound localization.

The probabilities of a switch in stimulus position to the left and to the right should be equal, and the positions of standard and test stimuli should vary. Both suggested standards would decrease the possibility of predicting stimulus position or the direction of the switch in stimulus position. *Experiment 1* showed that stimulus repetitions may decrease the variance in the internal representation of a stimulus, so only a single test stimulus should be presented in each trial. After the presentation of this test stimulus, no standard stimuli should be presented to avoid multiple switches in stimulus position. The response interval following the test stimulus should not be longer than the rate of stimulus repetition, since otherwise subjects can use the end in the sequence of stimuli (i.e., the absence of a stimulus) as a cue for responding.

Experiments should measure acuity with a difference detection paradigm and not with a left/right discrimination paradigm since a left/right discrimination paradigm allows subjects to ignore the standard stimulus to improve performance when the position of the standard stimuli is predictable. Furthermore, cognitive demands are lower in a difference detection paradigm than in a left/right discrimination paradigm.

The analysis should relate responses to the angular separation in sound source position in each trial. To ensure comparability of thresholds across studies, the threshold criterion should correspond to a d' of 1.0. Importantly, the effect of standard stimulus presentations should be analysed since repeated standard stimuli may improve the internal representation of standard stimulus position and thus acuity (see *Experiment I*). Reported results should include the acuity for one standard stimulus presentation prior to the test stimulus, since this measure is not influenced by the effect of standard stimulus repetitions on the internal representation of the standard stimulus position. Following this method would enable meaningful comparisons of acuity to precision, i.e. the internal spatial representation of a single stimulus, measured in studies with absolute tasks.

# Suggestion for standards in experiments on localization relative to a non-acoustic reference

The other type of relative task in the revised classification of sound localization tasks (see Chapter 3.5.2) corresponds to localization relative to a non-acoustic reference. *Experiment III*, which measured sound localization thresholds with this type of task in the European starling, is in line with all of the suggested standards for this type of task listed in Table 3.4.

**Table 3.4**: Suggestion for standards in experiments on localization relative to a non-acoustic reference. The colours represent suggestions for standards in the stimulus presentation (blue), the procedure (green) and the analysis (red). For details, see text.

	Stimuli		
Suggestion for standard	Procedure	Rationale	
	Analysis		
Shield sound sources from view		Unpredictable stimulus position	
Include broadband noise		Measures best localization performance subject is capable of	
Include tones, e.g. between 1 and 4 kHz		Measures influence of ITD and IID on localization	
Present single stimulus in each tr	ial	Predictable variance of internal representation of stimulus	
Include stimuli from 0° azimuth		Improves measure of response bias	
Present stimuli in both directions with equal probability		Unpredictable stimulus position	
Relate responses to loudspeaker positions		Corresponds to task: Identification of direction of sound source position	
Threshold criterion d'=1.0 or equal		Comparable thresholds across studies	

With the same rationale as in the standards suggested for tasks measuring acuity discussed above, sound sources should be shielded from view and stimulus types should include broadband noise and pure tones (e.g. between 1 and 4 kHz). This would avoid predictability of stimulus positions, provide a meaningful characterization of the best localization the subject is capable of, and measure the influence of ITD and IID on sound localization.

In each trial, only a single sound should be presented from the single sound source position, since stimulus repetitions may decrease the variance in the internal representation of the position of the sound source and thus improve thresholds (as outlined above). Sound source positions should include 0° to provide a better measure of response bias, i.e., the tendency to respond to one side. To reduce predictability of sound source positions, stimuli should be presented from the left and from the right with equal probabilities.

Since the type of task may be solved by the comparison of sound source positions to a non-acoustic spatial frame of reference, the analysis of the results should relate responses to the loudspeaker positions. A standardized threshold criterion of d'=1.0 would allow meaningful threshold comparisons across studies.

## 3.6. CONCLUSION

Sound localization thresholds are often compared across studies with the unexpressed assumption that the procedures in the specific studies did not influence results. In my view, threshold comparisons should be made with much more caution regarding the specific procedures used in each study. The first part of this dissertation provided an overview over many of these differences between sound localization studies that are often unexpressed but may complicate threshold comparisons. One of these differences is the number of standard stimulus presentations in experiments on the localization of sound sources relative to other sound sources. In a sound localization experiment on acuity in the European starling, I showed that acuity improved with the number of standard stimuli. This finding has significant implications for interpreting results from similar studies with multiple standard stimuli: acuity may have been overestimated in these investigations. Future studies employing repeated standard stimuli should report the effect of the number of standard stimuli on acuity to provide thresholds that are better comparable to other studies. In another sound localization study with European starlings, I introduced a task on localization relative to a nonacoustic reference. The traditional classification of sound localization experiments into two types, absolute localization and localization relative to another sound source, does not include this type of task. Thus, I revise this traditional concept and challenge the idea that the number of stimuli presented in each trial indicates whether the type of task is absolute or relative. By suggesting standards for experiments on relative sound localization, I provide a guideline which allows for a better comparability of results across future studies on sound localization.

To generalize the findings from *Experiment I* on the effect of the number of standard stimulus presentations on acuity in the European starling, an important next step would be a replication of this effect in humans as well as in other animals. In a difference detection paradigm with a variable number of standard stimuli, I hypothesize an improvement in acuity with an increase in the number of standard stimulus presentations. Under the assumption that the variance in the internal representation of standard stimulus position increases with an increase in the time period between standard stimuli, the time course of this variance in the internal representation may be investigated by varying the time period between standard stimuli.

As outlined above, the relationship between precision and acuity is still under debate and previous measures of acuity may have been overestimated. To clarify this relationship, precision and acuity need to be measured under similar experimental conditions while avoiding an overestimation of acuity. The experiment on acuity should employ a sound localization task relative to another sound source following the standards suggested above. Acuity measured with a single standard stimulus would allow for a meaningful comparison to precision unbiased by the effect of the number of standard stimulus presentations.

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# 4. METHODS IN SOUND LOCALIZATION: AUDITORY REPRESENTATIONAL MOMENTUM

The memory for the final position of a moving target tends to be displaced in the direction of motion (Figure 4.1). This effect of forward displacement has been referred to as the representational momentum effect (RM), suggesting a mental representation of the momentum of the moving target (Freyd & Finke 1984). RM has been found in the auditory, the visual and the tactile modality (for review, see Hubbard 2010) and is typically in the order of magnitude of a few degrees. Visual RM has been the subject of considerable research, which has identified a number of variables influencing the size of visual RM, including target characteristics and the type of response measure (for review, see Hubbard 2005). For example, the size of visual RM increases with target velocity (Freyd & Finke 1985; Finke et al. 1986; Freyd & Johnson 1987; Hubbard & Bharucha 1988; Hubbard 1990; Hubbard 1996; Munger & Minchew 2002; Munger & Owens 2004) and is larger when measured in action paradigms than in perceptual paradigms (Kerzel 2003; Kerzel & Gegenfurtner 2003). The computational theory of displacement (e.g., Hubbard 2005; Hubbard 2010) proposes that RM bridges the gap between perception and action and is based on a high-level predictive process. For example, catching a ball requires a sequence of perceptual, cognitive and motor processes beginning with the identification of the position of the ball and ending with the impact of the ball in the hand. Since this sequence of processes requires time, when the hand reaches out to catch the ball, the ball has already moved away from the position at the beginning of the sequence of processes. In order to bridge the time period between initial perception and final action, tasks like catching a ball require the prediction of future object paths. For example, the hand can reach out to a position where the ball is going to be.



**Figure 4.1:** The representational momentum effect. In this example, a target moves translationally with a rightward direction (black arrow) and terminates at a position indicated by the black vertical line. Observers tend to mislocalize the endpoint of the moving target as being further along the trajectory of motion, indicated by the blue dashed vertical line.

In contrast to the visual modality, only few studies investigated auditory RM (Perrott & Musicant 1977; Mateeff & Hohnsbein 1988; Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009; Schmiedchen et al. 2013). Most hypotheses on visual RM extend to RM in other modalities (Hubbard 2010), so similar effects in visual and

auditory RM may allow auditory motion research to benefit from the large amount of research and hypotheses on visual motion processing. However, the few studies on the effect of target velocity on auditory RM have reported ambiguous results, which do not match the increase in visual RM with target velocity. Thus, the effect of target velocity on the size of auditory RM remains unclear. In the following, I will discuss disadvantages in the methods of previous studies on auditory RM which may account for the difference in the reported effect of target velocity on RM between the auditory and the visual modality. I will present *Experiment IV* which investigated the effect of target velocity on auditory RM while avoiding these potential disadvantages. I will relate findings from *Experiment IV* to those of previous studies on visual and auditory RM.

#### 4.1. POTENTIAL DISADVANTAGES OF METHODS IN AUDITORY RM EXPERIMENTS

#### 4.1.1. Setup

Research on auditory RM requires the generation of moving targets. Free-field targets can be presented by a loudspeaker on a boom that may confound results through interfering mechanical sounds (Perrott & Musicant 1977; possibly also Mateeff & Hohnsbein 1988). Free-field targets can also be presented by an elaborate setup with multiple immobile sound sources that requires a large number of loudspeakers and limits spatial resolution (Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009; Schmiedchen et al. 2013). Target presentation via headphones allows for a better control of the stimulus, and externalized sound perception can be achieved by combining the raw signal with the Head-Related Transfer Function specific to the position in space. This method is termed "Virtual Auditory Space" (VAS) and has been established in auditory research in humans as well as in other species (for reviews, see for example Carlile 1996; Hausmann & Wagner 2011). *Experiment IV* used VAS to present targets via headphones (Figure 4.2).

#### 4.1.2. TARGET CHARACTERISTICS

The influence of the amount of spatial information provided by moving targets on the size of auditory RM is unclear. As described in Chapter 2.3, the spectrum of the sound defines the binaural and monaural localization cues of the target and thus represents a major factor influencing spatial target information. *Experiment IV* presents broadband noise targets to provide the full range of localization cues. Previous studies on auditory RM have limited localization cues by presenting pure tones (Perrott & Musicant 1977; Mateeff & Hohnsbein 1988) or bandpass noise (i.e. noise limited in frequency range;

Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009; Schmiedchen et al. 2013), which may have biased results.

Another factor influencing spatial information of the target in studies on auditory RM is the region in which the target ends. Frontal localization is superior to lateral localization (e.g., Carlile et al. 1997), so that targets ending laterally provide less precise spatial information about the target endpoint position than targets ending in the frontal region. This may be a factor underlying the difference in the effect of target velocity on auditory RM found in the study by Schmiedchen et al. (2013): targets ending in frontal regions showed a positive relationship of target velocity and the size of RM, while the size of RM decreased with target velocity for targets ending in lateral regions. *Experiment IV* avoids this disadvantage by presenting all target endpoints in frontal regions to minimize a potential bias of limited spatial information of target endpoints.

# 4.1.3. PROCEDURE

Studies on visual and auditory RM employ one of two types of response measure: action paradigms or perceptual paradigms (e.g., Hubbard 2005). In action paradigms, the subject indicates the endpoint of the moving target through a motor response (e.g., pointing). In perceptual paradigms, the subject reports the endpoint of a moving target through comparison to a probe (e.g., a numerical scale). In studies on visual RM, action paradigms result in larger size of RM than perceptual paradigms (Kerzel 2003; Kerzel & Gegenfurtner 2003). Getzmann & Lewald (2007) measured the perceived position of an *ongoing* moving auditory target with action and perceptual paradigms and found similar differences between the two paradigms. This indicates that action paradigms may result in larger sizes of auditory RM than those found in perceptual paradigms. Possibly, results from studies on auditory RM employing action paradigms (Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009; Schmiedchen et al. 2013) may have been biased by motor errors. To avoid the potential influence of motor errors, *Experiment IV* employed a perceptual paradigm in which subjects reported the endpoint of the target by referencing to a numerical scale (Figure 4.2).

Another potential factor influencing results on auditory RM measured in perceptual paradigms is the presentation of salient visual probe stimuli such as LEDs. These salient probes can evoke a ventriloquism effect, i.e. a shift in perceived position of an auditory towards a synchronous visual stimulus (Howard & Templeton 1966; Witten & Knudsen 2005; Getzmann & Lewald 2007). This potential ventriloquism effect may have affected the size of auditory RM reported in the study by Mateeff & Hohnsbein (1988). In *Experiment IV*, I minimized this potential bias by using a dimly lit numerical scale as a

reference for perceived target endpoints and switching off the roomlight during the experiment (Figure 4.2).

## 4.1.4. ANALYSIS

The localization of sounds can be biased by a constant shift of the perceived target position: for example, a target can constantly be mislocalized towards the right. In studies on auditory RM, this effect may bias the reported endpoint of moving targets. Measuring the localization of stationary targets in the region where the moving target ended allows for correcting reported moving target endpoints for this potential bias. In the analysis, the reported target endpoints are corrected by the constant shift in localization of the stationary targets. Except for the experiments by Perrott & Musicant (1977) and Mateeff & Hohnsbein (1988), all previous studies on auditory RM presented stationary targets that allowed correcting for this potential bias. *Experiment IV* presents stationary targets as well in order to correct reported target endpoints by this potential constant shift in localization.

### 4.2. MAJOR GOALS

Previous studies yielded ambiguous results on the effect of target velocity on auditory RM (Perrott & Musicant 1977; Getzmann et al. 2004; Schmiedchen et al. 2013), while studies on visual RM showed an increase in the size of RM with target velocity (e.g., Hubbard & Bharucha 1988; see Hubbard 2005). This difference may have resulted from several disadvantages in the methods of these auditory studies, including limited spatial target information and action paradigms that introduced motor errors. To provide an unbiased measure of the effect of target velocity on auditory RM, the present experiment investigates the effect of target velocity on auditory RM with the full range of localization cues and a perceptual response measure. This study is also the first to investigate a sensitive auditory effect such as auditory RM through VAS.

#### 4.3. EXPERIMENTAL PARADIGM

For target presentation through VAS, head-related transfer functions of each individual participant were recorded prior to the experiment or were available from the database of the Auditory Neuroscience laboratory (for details of the recordings, see Carlile & Blackman 2014). In the experiment, participants sat facing a numerical scale (Figure 4.2). In each trial, they were instructed to fixate one of three fixation crosses on the numerical scale which were located in the frontal region of the participant. Afterwards, a moving target was presented through VAS with one of three velocities (25°/s, 50°/s,

 $100^{\circ}$ /s). It began moving at  $\pm 90^{\circ}$  towards the midline and ended within  $\pm 2^{\circ}$  of the fixation cross. Participants were instructed to read out aloud the number on the numerical scale that corresponded to the perceived endpoint of the moving target. In each session, a block of stationary targets followed the block of moving targets. Similar to the instructions for reporting the endpoint of moving targets, participants were instructed to report the perceived position of the stationary target by referencing to the numerical scale. In the analysis of the RM, reported endpoints of moving targets were corrected for potential constant shifts in auditory localization.



**Figure 4.2:** Photographs of the setup for the experiment on the effect of target velocity on auditory representational momentum. a) Participants were seated in the centre of the numerical scale, with the chin on the chinrest. One hand carried a button to start a trial. A headtracker mounted on top of the headphones controlled for head position, and a LED device on top of the numerical scale provided feedback on deviation from initial head position. The photograph was taken prior to the beginning of the session with the roomlight switched on. b) The roomlight was switched off during the experiment avoid salient visual cues. LEDs illuminated the numerical scale from behind.

#### 4.4. SUMMARY OF THE RESULTS

In the present study which employed VAS, localization precision for stationary targets was similar to results from previous studies with loudspeakers in the free field (e.g., Makous & Middlebrooks 1990; Carlile et al. 1997).

Auditory RM linearly increased with an increase in target velocity: the RM effect reached +0.88° for a target velocity of 25°/s, +1.26° for a target velocity of 50°/s, and +2.27° for a target velocity of 100°/s. RM was not influenced by target direction or fixation point. Also, the interaction of these two factors did not influence RM, which indicates that the length of target trajectory and target duration did not affect auditory RM. This lack of an interaction effect also shows that the size of RM was similar for targets ending with movement towards the midline and targets ending with movement towards the periphery. The effect of eye position on the localization of the

endpoint was similar for moving and stationary targets: localization was consistently shifted towards the fixation point.

## 4.5. DISCUSSION

#### 4.5.1. Comparison of results to previous findings on auditory and visual RM

The linear increase in auditory RM with target velocity in *Experiment IV* is in line with results from several previous investigations of visual RM (Freyd & Finke 1985; Finke et al. 1986; Freyd & Johnson 1987; Hubbard & Bharucha 1988; Hubbard 1990; Hubbard 1996; Munger & Minchew 2002; Munger & Owens 2004). The size of the RM effect ranged between +0.88° and +2.27° and is thus comparable to the sizes of visual RM reported: for example, Hubbard & Bharucha (1988) showed that an increase in target velocity from 5.8°/s to about 35°/s resulted in an increase in visual RM from +0.8° to +2.2°. The linear correlation between target velocity and auditory RM suggests that the momentum of moving objects is included in the prediction of object paths, as suggested by theories on visual RM (e.g., Hubbard 2005; Hubbard 2010). The close relationship between auditory RM in this study and visual RM found in previous studies suggests that neural mechanisms that encode visual and auditory motion are more similar than previously thought, which is in line with a growing body of evidence from other studies on auditory motion processing (see Deas et al. 2008).

The results in *Experiment IV* were not to be expected on the basis of findings from previous studies on auditory RM. The linear increase in auditory RM with target velocity does not correspond to results from previous studies on this effect (see Table 4.1). Perrott & Musicant (1977) did not find such an effect, and results from Getzmann et al. (2004) showed the opposite effect. Schmiedchen et al. (2013) found a similar effect for targets moving towards the midline but the opposite effect for targets moving towards the periphery. Another difference between results from *Experiment IV* and previous studies on auditory RM is that the size of RM in the present study (+0.88° to +2.27°) is exceeded by the largest sizes of RM reported previously (see Table 4.1). They reached +25° (Perrott & Musicant 1977), +11° (Mateeff & Hohnsbein 1988), +5° (Getzmann et al. 2004), +4° (Getzmann & Lewald 2007), +2° (Getzmann & Lewald 2009), and +11° (Schmiedchen et al. 2013). Importantly, in most of these studies, target velocity was lower (see Table 4.1) than the lowest velocity in our study (25°/s) that resulted in a mean RM of 0.88°. Possibly, a higher target velocity may have increased the sizes of RM even further in most of these studies.

Reference	Target spectrum	Target velocity	Representational momentum effect	
			Range	Effect of target velocity
Perrott & Musicant (1977)	500 Hz pure tone	90°/s to 600°/s	-11° to +25°	No apparent effect
Mateeff & Hohnsbein (1988)	400 Hz pure tone	15°/s	+10° to +11°	
Getzmann et al. (2004)	1-3 kHz bandpass noise	8°/s and 16°/s	+1° to +5°	Decrease in RM with increase in target velocity
Getzmann & Lewald (2007)	1-3 kHz bandpass noise	12°/s	-4° to +5°	
Getzmann & Lewald (2009)	1-3 kHz bandpass noise	16°/s	0° to +2°	
Schmiedchen et al. (2013)	0.25-1 kHz or 2-8 kHz bandpass noise	13°/s to 160°/s	-1° to +11°	Motion towards midline: larger RM for larger velocity Motion towards periphery: smaller RM for larger velocity

Thus, results from the *Experiment IV* are in line with results from the visual modality but not in agreement with previous auditory studies. A likely factor for the difference to auditory studies is that *Experiment IV* avoided potential disadvantages in the methods, as introduced in Chapter 4.1. In the following, I will focus on the influence of spatial information on auditory RM which probably represents the most important factor for the differences in results to previous studies on auditory RM.

#### 4.5.2. EFFECT OF SPATIAL TARGET INFORMATION ON AUDITORY RM

One of the most important differences between Experiment IV and previous studies on auditory RM is the difference in spatial information of the target endpoint. One major factor influencing this spatial information is the target spectrum. As shown in Table 4.1, Perrott & Musicant (1977) used 0.5 kHz and pure tones as targets and found RM to range between -11° and +25°. Similarly, Mateeff & Hohnsbein (1988) employed 0.4 kHz pure tone targets that resulted in a RM range between +10° and +11°. Subsequent studies by Getzmann and colleagues (Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009) presented bandpass noise limited to 1-3 kHz. RM ranged between +1° and +5°, -4° to +5°, and 0° to +2°, respectively. Schmiedchen et al. (2013) used bandpass noise targets limited to 0.2-1 kHz or 2-8 kHz and found RM to range between -1° and +11°. Thus, all these studies with limited target spectra found larger sizes of RM and a larger range of RM than Experiment IV that presented broadband noise targets which provided the full range of localization cues. Also, sizes of RM were larger in studies presenting pure tones as targets (Perrott & Musicant 1977; Mateeff & Hohnsbein 1988) than in most studies presenting bandpass noise targets (Getzmann et al. 2004; Getzmann & Lewald 2007; Getzmann & Lewald 2009). These results suggest that the size of RM decreases with an increase in the localization cues provided by the target spectrum. This may indicate that the auditory system relies more on the

predictive mechanism responsible for the RM effect when the target position is more ambiguous.

Besides the target spectrum, another factor influencing spatial information of moving targets is the acuity of the auditory system. In line with results from Experiment IV, Schmiedchen et al. (2013) found an increase in the size of auditory RM with an increase in target velocity for targets moving towards the midline. However, in contrast to results from Experiment IV, the authors showed a negative relationship between target velocity and the size of RM for targets moving towards the periphery. This may be explained by the difference in target trajectory between the two studies. In Schmiedchen et al. (2013), targets moving towards the periphery ended far more peripherally than in Experiment IV. In their study, the decrease in the size of RM with an increase in target velocity was most pronounced for the most lateral target endpoints at  $\pm 85^{\circ}$ . In contrast, targets ending with movement towards the periphery in Experiment IV terminated at about ±25°. In the frontal region at ±25°, localization precision is better than in the peripheral region at ±85° (e.g., Carlile et al. 1997). Possibly, the poor localization precision at the lateral target endpoints in the study by Schmiedchen et al. (2013) may account for the difference in the effect of target velocity on auditory RM for targets moving towards the periphery compared to Experiment IV.

However, if the predictive component in the processing underlying the RM effect increases with a decrease in spatial information, as suggested by the effect of target spectrum on auditory RM discussed above, the size of RM should have increased and not decreased at target endpoints at ±85° in the study by Schmiedchen et al. (2013). One potential explanation is that targets ending at these lateral positions did not evoke a reliable perception of a moving sound. For example, targets ending at +85° started moving at +47°. These targets only moved in lateral regions where localization precision is lower than in frontal regions (e.g., Carlile et al. 1997). Grantham (1986) showed that at lateral positions, the trajectory length of a moving target needed to be larger than 30° to evoke the perception of a moving target. Thus, targets moving towards the periphery in the study by Schmiedchen et al. (2013) have possibly been insufficient to evoke a reliable perception of a moving sound. Furthermore, the fastest targets (that resulted in the lowest RM) reached durations of only 0.25 s, which is in the range of the minimum stimulus duration required to evoke the perception of moving sound (Grantham 1986). Thus, poor spatial target information and short target durations of fast moving stimuli in the study by Schmiedchen et al. (2013) may explain the difference to results from Experiment IV.

# 4.6. CONCLUSION

Previous studies on auditory RM showed larger RM effects than visual RM studies, and did not confirm an increase in the size of RM with target velocity that has been found in many studies on visual RM. The present experiment avoids common disadvantages of the methods used in studies on auditory RM. Unlike results from previous studies on auditory RM, results show an auditory RM effect similar to the visual RM effect: the range of RM was similar, and the size of RM linearly increased with target velocity. This indicates that auditory and visual RM may depend on similar processing mechanisms. Comparisons to previous studies on auditory RM. Possibly, the predictive component in the mechanism underlying RM increases with an increase in the ambiguity of target position.

The present experiment is the first to show that VAS allows investigating a sensitive effect such as auditory RM, so future studies can employ this method to investigate auditory RM and similar perceptual effects. One possible next step in research on auditory RM is a clarification of the role of spatial target information on the size of auditory RM. As outlined above, a decrease in target spectrum and therefore in localization cues may increase the predictive component of the mechanism underlying auditory RM. I hypothesize that RM is larger for tones than for broadband noise measured under the same experimental conditions.

Another focus of future experiments on auditory RM may be the effect of vertical target movement. Visual RM is smaller for upward and larger for downward movement (e.g., Hubbard & Bharucha 1988; see Hubbard 2005), an effect also known as "representational gravity". The hypothesis of similar processing mechanisms underlying auditory and visual RM predicts similar effects of vertical target movement on auditory RM. Also, an auditory representational gravity effect would show that auditory RM is not only restricted to binaural localization cues but also can be evoked with monaural localization cues.

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# 5. Concluding remark

This dissertation demonstrates how methods commonly employed in studies on the localization of static sounds or on auditory RM can affect results and therefore complicate comparisons of results across studies. In the first part of this dissertation, I discussed the differences between paradigms used to study the localization of static sound sources and pointed out how these may influence results. One of the often unexpressed differences between paradigms is the repetition of stimuli in many previous studies on acuity. I showed that stimulus repetitions can improve acuity, which suggests that in many previous investigations this measure may have been overestimated. Further, I revised the traditional classification of sound localization tasks and provided a guideline for experiments on relative sound localization. In the second part of this dissertation, I discussed potential disadvantages in studies on auditory RM and presented an experiment that avoided these disadvantages. The similarity of results to visual RM suggests that the methods were well-suited to investigate auditory RM.

In my view, experiments on sound localization that are carried out with detailed attention to the methods allow for the most meaningful interpretation of results. As I have outlined above, experimenters should carefully choose stimulus characteristics, be aware of how the procedure in the paradigm employed may influence results, and should choose an analysis that is appropriate for the type of task. As reviewed in this dissertation, previous sound localization studies used a multitude of stimuli and procedures that complicate comparisons of results across studies. Furthermore, many did not control for potential influences of methods on results or employed inappropriate analyses. I hope that this dissertation represents an important step towards a closer attention to the methods used in future sound localization research.

# 6. EXPERIMENT I: AZIMUTHAL SOUND LOCALIZATION IN THE EUROPEAN STARLING (*STURNUS VULGARIS*): II. PSYCHOPHYSICAL RESULTS

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## 6.1. Abstract

Small songbirds have a difficult analysis problem: their head is small compared to the wavelengths of sounds used for communication providing only small interaural time and level differences. Klump and Larsen (1992) measured the physical binaural cues in the European starling (Sturnus vulgaris) that allow the comparison of acoustical cues and perception. We determined the starling's minimum audible angle (MAA) in an operant Go/NoGo procedure for different spectral and temporal stimulus conditions. The MAA for broadband noise with closed-loop localization reached 17°, while the starling's MAA for open-loop localization of broadband noise reached 29°. No substantial difference between open-loop and closed-loop localization was found in 2 kHz pure tones. The closed-loop MAA improved from 26° to 19° with an increase in pure tone frequency from 1 to 4 kHz. This finding is in line with the physical cues available. While the starlings can only make use of interaural time difference cues at lower frequencies (e.g., 1 and 2 kHz), additional interaural level difference cues become available at higher frequencies (e.g., 4 kHz or higher, Klump and Larsen 1992). An improvement of the starling's MAA with an increasing number of standard stimulus presentations prior to the test stimulus has important implications for determining relative (MAA) localization thresholds.

## 6.2. INTRODUCTION

The discrimination of sound source locations highly benefits birds engaging for example in territorial or predator-prey interactions (Klump 2000). Since songbird head sizes are small compared with the wavelengths of communication sounds, their auditory system faces a difficult analysis problem. In the hearing range of the European starling (Sturnus vulgaris), the maximum difference in sound pressure level between the frontal speaker position and other speaker positions ranges from about 2 to 11 dB for 1 to 8 kHz, respectively, therefore, the interaural intensity difference (IID) in general increases with frequency (Klump and Larsen 1992). The maximum interaural time difference (ITD) is about 100 µs (Klump and Larsen 1992), and both cues are thought to be used by birds for sound localization (Klump 2000). It has been suggested that the avian interaural canal turns the eardrums into pressure difference receivers and may provide for a physical mechanism that helps coping with the challenge of a small head size, though this is still in debate (e.g., see review by Klump 2000). For describing the cues available for sound localization, Klump and Larsen (1992) measured the binaural cues in the auditory system of the European starling and concluded that starling ears are functionally decoupled, with the median interaural attenuation increasing from 12.3 dB at 1 kHz to 16.8 dB at 4 kHz. Here, we investigate the minimum audible angle (MAA) in the European starling using operant conditioning techniques and compare the available physical cues with the starling's perception. The

MAA paradigm (Mills 1958) provides reference stimuli and the subject needs to report a change in the location of the sound source. It differs from tasks determining the minimum resolvable angle (MRA) that present sounds from only one source out of two or more sources at different positions and the subject is forced to indicate at which position the active source was located (e.g., see Klump 2000). Besides the 1, 2 and 4 kHz tones that represent stimulus types from Klump and Larsen (1992), we used broadband noise stimuli that provide rich spectral cues. To compare the MAA under open-loop and closed-loop conditions, we investigated the effect of reducing the stimulus duration from 1 to 0.1 s on the starling's MAA for 2 kHz tones and broadband noise.

#### 6.3. MATERIALS AND METHODS

#### 6.3.1. SUBJECTS

Four adult, wild-caught European Starlings (2 males and 2 females) that were naïve with respect to psychoacoustical experiments participated in this study. Their ages ranged from at least 1 year to at least 5 years. They were kept in individual cages (1.5 m W x 1.0 m H x 0.7 m D) with water ad libitum. Natural and artificial light illuminated the room for at least 15 h a day. The food consisted mainly of duck-food pellets (Agravis Geflügelfinisher) and was supplemented by cod liver oil and vitamins. Food was restricted, during the experiments the birds were kept at 92–96 % of their free-feeding weight. Supplementary food was provided in the evening after the test sessions. The starling weight was checked daily. At least twice a week we provided them with the possibility to take a bath. A wire cage (0.2 m W x 0.2 m H x 0.3 m D), which the birds entered voluntarily allowed us to transport the birds from their cages to a soundproof test chamber that was located in the neighboring room.

#### 6.3.2. Setup

The experiments took place in a soundproof chamber (1200-A series, Industrial Acoustics Company, England; inside dimensions:  $1.2 \text{ m W} \times 1.9 \text{ m H} \times 1.0 \text{ m D}$ ) equipped with a 15 cm thick layer of sound-absorbing foam consisting of a 5 cm layer with a flat surface (Plano 50/0, Seyboth, Germany) and a 10 cm layer with a pyramid-structured surface (Pyramide 100/50, Seyboth). Inside the chamber was a wire cage (0.5 m W x 0.8 m H) with two perches (8 cm W) and an opening (0.2 m W x 0.2 m H). Opposite to the opening the cage formed a horizontal semicircle (diameter = 0.5 m) with its center located at the position where a bird's head would be during the experiment (for a bird's view see Figure 6.1). Viewing from this position, the cage had an opening of 20 cm in height that was covered with acoustically transparent but

optically opaque cloth. Behind the cloth was a semicircle (diameter = 0.65 m) of 15 loudspeakers (Vifa XT25TG30-04, ASE, Germany).

To monitor the bird's behavior, the rear perch was equipped with a light barrier (Conrad Electronic, Germany) indicating when the bird sat on that perch. The front perch permitted access to a custom-built automatic feeder which contained 48 small cooked mealworms (Tenebrio molitor, Zoo Med's Can O' Mini Mealies, USA), i.e., the primary reinforcer delivered if the birds responded correctly to the given task (see below). Two LEDs (HighPower LED Spot, Lumitronix, Germany) containing diffuser lenses (Lumitronix) lit the chamber from the rear of the wire cage. An additional reward light, an LED-spot (Paulmann, Germany) at the back of the chamber, provided a secondary reinforcer. A webcam (QuickCam Pro 9000, Logitech, Switzerland) connected to an external Windows-operated laptop allowed to observe the bird's behavior during the experiment from a top view.



**Figure 6.1:** View on a starling participating in experiment. The bird's head facing towards 0° is in the center of the 13 horizontally aligned loudspeakers (center positions indicated by plus signs) all spaced 12.9° apart and hidden behind an acoustically transparent cloth. Red and blue plus signs show exemplary stimulus source locations for repeated standard and test stimuli in a trial based on a reference position of 6°. With an angular separation between standard and test stimulus of 12.9°, a change in location from left to right and a reference position at 6°, the repeated standard stimulus is presented at A7 (i.e., 0°) and the test stimulus at A8 (i.e., 12.9°). For further explanation see text

A Linux-operated computer controlled the experiment operating two enhanced realtime processors (RP2, Tucker Davis Technologies, USA). Two external soundcards (Hammerfall DSP Multiface II, RME, Germany) connected to two sound amplifiers (RMB-1048, Rotel, Japan) controlled 13 loudspeakers in the semicircle that we used in our experiments (the loudspeakers at the edge of the semicircle were not used).

## 6.3.3. Stimuli

Stimulus types comprised broadband noise signals (0.5-6 kHz) and tones (1, 2 and 4 kHz) with a total duration (including the ramps) of 1 s, as well as broadband noise and 2 kHz tones with a total duration of 100 ms. The soundcards generated new signals for each stimulus presented. Within a session, only one stimulus type was used. For two of the birds, all six stimulus types varied between the sessions. Two of the birds completed the 1 s stimulus types before starting with the 100 ms types. Each stimulus had 5 ms Hanning ramps and was calibrated to 63 dB SPL with a sound level meter (2238 Mediator, Brüel & Kjær, Denmark) by positioning the microphone in the center of the semicircle of loudspeakers where the bird's head would be located in the experiment. In order to rule out differences between loudspeaker characteristics as a discrimination cue, stimuli roved ±3 dB in level. In addition, one 256th order FIR filter adjusted the mean loudspeaker spectrum, and an additional 2nd order FIR filter for each of the 13 loudspeakers matched the level between loudspeakers. The coefficients were determined by individually calibrating each loudspeaker. The total level (post filtering) varied between loudspeakers by ±1.7 dB in the frequency range from 0.5 to 6 kHz. At 1, 2 and 4 kHz, the loudspeakers varied by 1.9, 1.9 and 2.2 dB, respectively. The frequency response of individual loudspeakers within the frequency range from 0.5 to 6 kHz varied by up to ±3.6 dB.

## 6.3.4. PROCEDURE

We trained the birds to report perceived changes in stimulus location in a Go/NoGo paradigm. The birds were conditioned to sit on the rear perch to start a trial with their head positioned at about the center of the semicircle. Video observation revealed a variation in head angle of less than about 30° with the birds mostly pointing their beak towards the most frontal loudspeakers. In test trials, the standard stimuli repeated every 2 s and were replaced by a single test stimulus from another location after 1–5 presentations. After the test stimulus, stimulus presentation stopped for at least 4 s. The angular separation between repeated standard and test stimuli covered six angles ranging from 12.9° to 90.0° and varied according to the method of constant stimuli. The direction of the change in stimulus location, i.e., a test stimulus to the right or to the left of the standard stimulus, was randomized between trials.

During a report phase of 2 s following the beginning of a test stimulus, the birds were to jump off the perch to report the perception of the change in stimulus location. If the birds jumped within the report phase, such a "hit" led to a reward in 80 % of all cases, and always the reward light lit for 5 s. If the birds did not jump during the report phase, such a "Miss" of a test stimulus initiated the beginning of the next trial. If the

birds jumped off the perch although no test stimulus was presented the chamber light was switched off for 5 s.

Sham trials in which the test stimulus location was equal to the standard stimulus location provided a measure for the false alarm rate. If the birds jumped off the perch during the report phase in a sham trial, such a "false alarm" switched off the chamber light for 5 s.

All 13 loudspeakers were potential sources of standard or test stimuli. For all stimuli presented, either the real loudspeaker position matched the stimulus location or both neighboring loudspeakers played identical stimuli simulating a sound source position between the loudspeakers given that birds have summing localization (e.g., see Keller and Takahashi 1996). Figure 6.2 shows the psychometric functions for all six stimulus types. The fact that in the psychometric functions the sensitivity for simulated sound source locations lies between that obtained with real sound source locations obtained at larger and smaller angular separation indicates that no substantial difference in perception between these two conditions exists. The probabilities of correct responses for absolute loudspeaker positions and stimulus sources according to summing localization do not differ in their residuals in relation to the psychometric function (p > 0.05, two-tailed t test for independent samples) indicating that there was no systematic bias with respect to the psychometric functions. Furthermore, the residuals were minute (0.0003 ± 0.0043 SE for absolute source locations and -0.0019 ± 0.0043 SE for source locations according to summing localization) indicating that the psychometric functions represented the complete data set quite well. Thus, it was feasible to improve the spatial resolution of stimulus presentation in the setup by simulating speaker positions by summing localization in addition to the absolute (real) loudspeaker positions.

In the study, we vary the reference position, which represents the average position of the speakers used for standard and test stimuli. The five different reference positions (-32°, -19°, 6°, 19° and 32°) allow evaluating the effect of sound presentation from frontal versus lateral sources. By randomly choosing the reference position from one trial to the next, the location of the sources for standard and test sounds was unpredictable for the birds. Figure 6.1 shows an example of a trial with the spatial locations of standard and test stimulus at a separation of 12.9° and the dotted line connecting the position of the bird's head with the reference position. With a change in location from left to right and a reference position at 6°, the repeated standard stimulus is presented at loudspeaker A7 and the test stimulus at loudspeaker A8. The reference position of 6° is very close to a frontal position at 0° and was chosen to present the smallest separation between standard and test stimulus locations of 12.9° for real (rather than simulated) loudspeaker positions. With only one reference position at 6°, the birds might have been able to predict the test stimulus location

based on the standard stimulus location. Hence, we picked one of the five reference positions at random.

A session comprised 100 trials and began with 10 warmup trials that featured the largest angular separation between standard and test stimulus. Those first 10 trials were not included in the data analysis. The following 90 trials consisted of 60 test trials and 30 sham trials. In test trials, all combinations of the six angular separations between standard and test stimuli and five reference positions were presented, with each combination occurring twice in each session. In the sham trials, no change in stimulus location was presented. The sequence of all trials, excluding the warm-up trials, was randomized in a session. The subjects could complete a session in approx. 30 min. Each starling conducted up to four sessions per day, with a minimum break of 1 h between the end of the last and the beginning of the next session.



**Figure 6.2:** The starlings' probability of correct response for the 6 angular separations between repeated standard stimuli and the test stimulus for the six stimulus types (mean ± SE), averaged across all reference positions and numbers of standard stimuli. The curves show the psychometric functions with a sigmoidal fit (see Lam et al. 1996). The adjusted R<sup>2</sup> is 0.981 for 1 s 1 kHz, 0.997 for 1 s 2 kHz, 0.982 for 1 s 4 kHz, 0.999 for 100 ms 2 kHz, 0.997 for 100 ms noise and 0.994 for 1 s noise. Filled circles represent angular separations between repeated standard and test stimulus presented from absolute loudspeaker positions, open circles represent simulated stimulus sources according to summing localization

#### 6.3.5. DATA ANALYSIS

The sensitivity measure d' (e.g., see Green and Swets 1966) indicated each subject's discrimination performance between standard and test stimuli, and this sensitivity was calculated separately for each angular separation between standard and test stimulus. The sensitivity d' for the starlings' threshold was 1.0. This threshold criterion allows

comparisons with results from other studies that used two-alternative forced choice procedures. In order to assure an accurate threshold determination we applied specific criteria to decide whether a session was valid and hence included in the data analysis. It was included if the subjects responded to no more than 10 % of the sham trials and to at least 70 % or, for a few sessions, 60 % of the test stimuli with the two largest angular separations between standard and test stimuli. Even with a response probability of 60 % and a false alarm rate of 10 %, d' reaches at least 1.5 and is therefore well above threshold. The birds reached a mean sensitivity d' of more than 2.2 for the two largest angular separations between standard and test stimulus in each of the six stimulus types. Each bird had to complete a total of six valid sessions for each of the six stimulus types. One bird succeeded to complete only four valid sessions for the 100 ms 2 kHz type, we included the results from these four sessions in the data analysis. In order to determine the MAA, we linearly interpolated the sensitivities d' of neighboring angular separations. In addition to the sensitivity, we calculated the criterion value c that reveals the subject's response propensity.

#### 6.4. Results

On average, each bird needed 17 sessions to reach the defined threshold for a stimulus type. The major reason for invalid sessions was an insufficient amount of hits for the two largest angular separations (32 % of all sessions). The mean false alarm rate of the valid sessions was 5.3 %. Figure 6.3 shows the mean thresholds of all four birds for the six stimulus types averaged across all reference positions and numbers of standard stimuli. For the 1 s pure tones, the starling's mean MAA reaches 26.4°, 24.2° and 19.3° for frequencies of 1, 2 and 4 kHz, respectively, and the mean MAA for the 100 ms 2 kHz tone was 27.4°. In the broadband noise types, the MAA reached 17.4° and 28.6° in the 1 s and the 100 ms type, respectively. Generally, the individual starling thresholds were more variable in the 2 kHz conditions.



**Figure 6.3**: The starlings' Minimum Audible Angle for the six different stimulus types (mean ± SE), averaged across all reference positions and numbers of standard stimuli

In a Generalized Linear Mixed Model ANOVA, we analyzed the factors influencing the starlings' MAA that represented the dependent variable in this analysis. The birds were included as a random effect and the stimulus type as a fixed main effect. The MAA differed between the six stimulus types (p = 0.011,  $F_{(5,18)} = 4.180$ ), and post hoc analyses showed that it was significantly better in the 1 s noise type than that in the 100 ms noise type (p = 0.036, t test, Bonferroni- corrected). Therefore, the starlings' MAA improved with longer stimulus duration in broadband noise. An additional Generalized Linear Mixed Model ANOVA treated the birds as a random effect and the frequency of the 1 s types for 1, 2 and 4 kHz as a covariate. Thresholds linearly improved with an increase in frequency from 1 to 4 kHz (p = 0.039,  $F_{(1, 7)} = 6.417$ ). Concluding from these results, the starlings improve their MAA with an increase in sinusoidal frequency from 1 to 4 kHz.

An additional Generalized Linear Mixed Model ANOVA analyzed the factors influencing the starlings' sensitivity. The birds were included as a random effect, while the stimulus type, the angular separation between standard and test stimulus, the reference position, and the number of standard stimuli presented prior to a test stimulus were treated as fixed main effects in the analysis. The birds did not differ in their sensitivity (p > 0.05), indicating no individual differences in perception. As expected from the differences in MAA between the stimulus types described above, the stimulus type affected the birds' sensitivity (p < 0.001,  $F_{(5,2,447)} = 27.185$ ). Psychometric functions like those shown in Figure 6.2 resulted from an effect of the angular separations between standard and test stimulus on the starling's sensitivity (p < 0.001,  $F_{(5,2,447)} = 467.686$ ). Also, the reference position affected the bird's sensitivity (p = 0.006,  $F_{(4,2,447)} = 3.606$ ). A post hoc analysis revealed no significant differences in the bird's sensitivity for different reference positions with an exception of the

comparison between a reference position of -19° and of -32° that correspond to mean sensitivities of 1.84 and 2.12, respectively (p = 0.005, t test, Bonferroni-corrected). There is no general trend in the starlings' sensitivity as azimuthal disparity increases, with the starlings' mean sensitivity reaching 2.02, 1.92 and 1.93 for reference positions of 6°, 19° and 32°, respectively. An effect of the number of standard stimulus presentations prior to a test stimulus on the birds' sensitivity (p < 0.001,  $F_{(4,2,447)}$  = 46.222) is shown in Figure 6.4. The starlings' sensitivity d' increased with an increasing number of standard stimulus presentations prior to the test stimulus. For example, for an angular separation between standard and test stimulus of 26° in the 1 s 4 kHz type, the mean sensitivity increased from 0.55 for 1 standard stimulus presentation to 1.72 for 5 standard stimulus presentations. Post hoc analyses of the Generalized Linear Mixed Model showed that sensitivity differed significantly between the first four standard stimulus presentations (all pairwise comparisons p < 0.05, t-tests, Bonferronicorrected). Figure 6.4 also shows an effect of the interaction of the stimulus type and the angular separation between standard and test stimulus (p = 0.001,  $F_{(25,2,447)}$  = 2.072) and an effect of the interaction of the stimulus type and the number of standard stimuli presented prior to a test stimulus on the birds' sensitivity (p < 0.001,  $F_{(20, 2, 447)} = 2.732$ ). Also, there was an effect of the interaction of the stimulus type and the reference position (p = 0.005,  $F_{(20, 2, 447)}$  = 2.002) and an effect of the interaction of the angular separation between standard and test stimulus and the number of standard stimulus presentations (p = 0.001,  $F_{(20, 2,447)}$  = 2.318), but none of these interactions showed a general trend of change in sensitivity.



**Figure 6.4:** The starlings' mean discrimination performance (sensitivity d') between standard and test stimulus for different stimulus types in relation to the angular separation and the number of standard stimulus presentations prior to a test stimulus, averaged across all reference positions

In an additional Generalized Linear Mixed Model, the number of standard stimuli represented a fixed effect, the birds were included as a random effect and we treated

the false alarm rate as the dependent variable. The number of standard stimulus presentations did not affect the false alarm rate (p > 0.05), i.e., the birds did not respond with different probabilities to no perceived change in stimulus location for all numbers of standard stimulus presentations. This does not mean that they keep their criterion constant, since the criterion does not only depend on the false alarm rate but also on the hit rate. A Generalized Linear Mixed Model analyzing the effect of the number of standard stimulus presentations on the criterion c as the dependent variable revealed a significant relationship (p < 0.001,  $F_{(4, 15)} = 12.477$ ). The criterion decreased from 1.02 for 1 standard stimulus presentation to 0.56 for 5 standard stimulus presentations the birds' criterion shifted closer to that of an ideal observer.

#### 6.5. DISCUSSION

In this study, we investigated the MAA of European starlings for stimulus types with different spectral properties and stimulus durations. The best MAA was observed for a 1 s broadband noise stimulus, a finding consistent with sound localization performance for broadband noise in other bird species being at least equal to or better than localization performance for sinusoidal stimuli. Some bird species also share with the starlings in our study an improvement in sound localization with an increase in sinusoidal frequency from 1 to 4 kHz. Exemplary studies that investigated sound localization in birds are summarized in Table 6.1. As we pointed out in the data analysis, we chose a d' threshold of 1.0 to compare our results to those studies that used Two-alternative forced choice paradigms. A d' of 1.0 corresponds to 0.76 probability of correct response in a Two-alternative forced choice paradigm. The threshold criteria of the Two-alternative forced choice studies cited in Table 6.1 ranged from 0.65 to 0.75 probability of correct response. Knudsen and Konishi (1979) used head turning accuracy as a measurement, and Bala et al. (2003) used a threshold criterion that corresponds to 0.75 probability of correct response. Therefore, our results are very well comparable to the results of the exemplary studies in Table 6.1.

**Table 6.1:** Sound localization accuracy for broadband noise and 1, 2 and 4 kHz tones measured in selected studies on different bird species. Two-alternative forced choice procedures are abbreviated as 2AFC, p(c) represents the probability of correct response

Species	N	Paradigm	Threshold criterion	Stimulus	Sound localization accuracy [°]	Reference
Barn owl ( <i>Tyto alba</i> )	1	MRA, Search coil	Head turning accuracy	1kHz, 1s	12	Knudsen & Konishi (1979)
				2kHz, 1s	10	
				4kHz, 1s	8	
				2kHz, 75ms	~12	
				4kHz, 75ms	~10	
				broadband noise, 1s	4	
				broadband noise, 75ms	~5	
Barn owl (Tyto alba)	3	MAA, Pupillary Dilation Response	D≥0.8, i.e., 0.75 p(c)	broadband noise, 100ms	3	Bala et al. (2003)
Bobwhite quail (Colinus virginianus)	2	MRA, 2AFC	0.75 p(c)	1kHz, <10s	~180	reanalysis of data by Gatehouse & Shelton (1978)
				2kHz, <10s	~50	
				50ms broadband noise pulses, <10s	~90	
Budgerigar ( <i>Melopsittacus</i> <i>undulatus</i> )	3	MRA, 2AFC	0.75 p(c)	1kHz, 200ms	69	Park & Dooling (1991)
				2kHz, 200ms	36	
				4kHz, 200ms	25	
				broadband noise, 200ms	29	
Canary (Serinus canarius)	2	MRA, 2AFC	0.75 p(c)	1kHz, 200ms	71	Park & Dooling (1991)
				2kHz, 200ms	55	
				4kHz, 200ms	49	
				broadband noise, 200ms	27	
European starling (Sturnus vulgaris)	4	MAA, Go/NoGo	d'=1.0, equivalent to 0.76 p(c) in a 2AFC procedure	1kHz, 1s	26	the present study
				2kHz, 1s	24	
				4kHz, 1s	19	
				2kHz, 100ms	27	
				broadband noise, 1s	17	
				broadband noise, 100ms	29	
Great tit ( <i>Parus</i> major)	2	MRA, 2AFC	0.65 p(c)	1kHz, 300ms	26	Klump et al. (1986)
				2kHz, 300ms	20	
				4kHz, 300ms	24	
				broadband noise, 300ms	21	
Zebra finch ( <i>Taeniopygia guttata</i> )	3	MRA, 2AFC	0.75 p(c)	1kHz, 200ms	180	Park & Dooling (1991)
				2kHz, 200ms	88	
				4kHz, 200ms	71	
				broadband noise, 200ms	101	

In conclusion, the MAA sound localization results in the European starling in our study are in the range of values for the accuracy of sound localization of other bird species with equally small head size. However, most of these species showed a worse sound localization compared to that of starlings (with a possible exception of the eastern towhee, see Nelson and Suthers 2004). The improvement in the starling's MAA with an increase in sinusoidal frequency from 1 to 4 kHz is expected from the variation of physical interaural cues in relation to frequency.

## 6.5.1. Comparison of localization performance with physical binaural cues

The first important binaural cue available to the auditory system for localizing sound in azimuth is the ITD. Models of azimuth sound localization based on ITD evaluate the ability to represent the interaural phase differences by the auditory neurons. Peripheral neurons in the starling code the phase reliably only for frequencies of up to

3 kHz (Gleich and Narins 1988), with the vector strength of phase locking decreasing from 0.9 at 0.4 kHz to <0.3 at 3 kHz. At a constant ITD, however, the corresponding difference in phase angle increases with increasing frequency leading to larger interaural phase difference cues for higher frequencies (e.g., see Knudsen 1980). Both effects have to be kept in mind when evaluating the usefulness of ITD cues. Klump and Larsen (1992) calculated ITDs for 1, 2 and 4 kHz in the starling using the model by Calford and Piddington (1988) and predicted larger maximum ITD cues for lower frequencies. The ITD for a stimulus with 90° azimuth ranged from about 109 µs for 1 kHz to about 67 μs for 2 kHz and 55 μs for 4 kHz. At the starling's MAA, the predicted ITD is about 50, 25 and 17 µs for 1, 2 and 4 kHz stimuli, respectively. This corresponds to interaural phase differences of 18°, 18° and 24° for 1, 2, and 4 kHz stimuli, respectively. These ITD model calculations including the effect of interaural transmission in the starling match those excluding interaural transmission: Based on the calculations in the model proposed by Kuhn (1977) assuming that the head is a sphere, the MAA at 1, 2 and 4 kHz corresponds to an ITD of about 30, 28 and 22  $\mu$ s. This also indicates no major effect of the interaural canal on ITD cues. Klump and Larsen (1992) and Welch and Dent (2011) pointed out, however, that the spherical head model may be too simple to provide an accurate estimate of the ITD cues. In the budgerigar, the MRA at 1, 2 and 4 kHz equals ITD cues of 62, 54 and 50 μs for 1, 2 and 4 kHz tones, respectively (Park and Dooling 1991). The same study investigated the MRA in the canary that corresponded to ITD cues of 55, 35 and 25  $\mu$ s for 1, 2 and 4 kHz, respectively, and in the zebra finch that reached MRAs that equal ITD cues of 52 and 49  $\mu$ s for 2 and 4 kHz, respectively (Park and Dooling 1991). Klump et al. (1986) found MRAs in the great tit that corresponded to ITD cues of 24, 18 and 22  $\mu$ s for 1, 2 and 4 kHz, respectively. Based on the localization error in barn owls for broadband noise 10° from the fixation point (Knudsen et al. 1979) Knudsen (1980) calculated a threshold ITD of 8 µs in the barn owl. This overview suggests that in a frequency range in which a good representation of stimulus phase by the auditory nerve is provided the ITD cues in the starling and other bird species may be sufficient to localize sounds. This hypothesis is supported by the observation that budgerigars successfully lateralize a sound based on ITDs of less than about 30 µs (Welch and Dent 2011). In conclusion, based on the behaviorally measured MAAs and the corresponding available physical cues, the starlings can make use of ITD and interaural phase difference cues for localizing sound of up to 2 or 3 kHz. The strong reduction of vector strength above frequencies of 3 kHz renders it unlikely that the starlings used these cues for the 4 kHz stimuli in the experiments, though.

The IID represents the second important binaural cue for sound localization. Klump and Larsen (1992) showed that laser vibrometry measurements of the tympanum vibration in the starling's right ear resemble probe microphone measurements of the sound pressure at the right ear's meatus indicating that starlings have functionally decoupled ears. The probe microphone measurements revealed that the IID increases with the azimuth angle of stimulus presentation and with an increase in frequency from 1 to 8 kHz. While in these measurements the average change in sound pressure level for frontal stimuli (-60° to +60° in azimuth) were only 0.006 dB per degree for 1 kHz tones, they reached 0.053 dB per degree for 8 kHz tones. Since the birds were able to freely move their head, the change in sound pressure level per degree could even be larger at 4 kHz stimuli and reached up to about 0.2 dB per degree (see laser vibrometry measurements for 4 kHz tones shown in Fig. 1 in Klump and Larsen 1992). In the psychophysical experiments presented here, the starling's MAA linearly improved from 26.4° to 19.3° with an increase in frequency from 1 to 4 kHz. Using the model by Duda and Martens (1998) based on a spherical geometry of the head, the starling's MAA at 1, 2 and 4 kHz correspond to IID cues of about 0.09, 0.12 and 0.43 dB, respectively. While the IIDs at 1 and 2 kHz appear to be too small to provide a useful cue, at 4 kHz a sufficiently large IID may be available to the starlings. Welch and Dent (2011) observed that in the budgerigar IIDs of between 0.5 dB for broadband noise and 1–2 dB for pure tones of 1–4 kHz were sufficient for lateralizing a sound source. Also the pigeon (Columba livia, Lewald 1987a) could lateralize a sound source if provided with an IID of between 1.5 and 2.5 dB (median values, IID thresholds as low as 1 dB were observed in individual birds).

In summary, the ITD and IID cues available to the starling can explain the decrease in MAA with an increase in frequency from 1 to 4 kHz. At a frequency of 1 kHz, the starling mostly can make use of ITD to localize sounds, and given sufficient vector strength for accurate localization an improvement of the MAA at 2 kHz could be explained. With an increase in frequency to 4 kHz, ITDs are not likely to provide useful cues since phase locking of starling auditory nerve fibers is compromised at this frequency (Gleich and Narins 1988). IID cues, however, increase with frequency and the MAA at 4 kHz could be explained by the IID thresholds observed in the lateralization experiments. In general, the ITD and IID cues available to the starling match the behaviorally measured MAA thresholds.

## 6.5.2. EFFECT OF REPEATED PRESENTATIONS OF STANDARD STIMULI ON LOCALIZATION SENSITIVITY

Our study shows that the number of standard stimulus presentations prior to a test stimulus affects the starling's MAA. This finding is consistent with the observation that repeated motifs occur in starling song (e.g., Eens et al. 1991) that may improve judging song diversity (Zokoll et al. 2007). Like in the starling MAA experiment in the present study, starling auditory memory depends on the number of standard stimulus presentations (Zokoll et al. 2007, 2008).

The starlings' false alarm rate did not depend on the number of standard stimulus presentations. However, the criterion shifted towards that of an ideal observer with an increase in the number of standard stimulus presentations. This conclusion based on the observation of hit and false alarm rates assumes that the probability distributions used in signal detection theory to calculate the criterion do not change with repeated presentations. However, an increase in sensitivity with an increase in the number of standard stimulus presentations is just what one would expect if the birds build templates of the standard stimulus that they improve with each repetition (e.g., Deutsch 1970; for an overview, see Zokoll et al. 2007). This expectation is in line with observations on the detection of deviants in studies employing an oddball paradigm and using different patterns of stimulus variation over time (Bendixen et al. 2007). A reduction of the variance of the representation of the standard stimulus resulting from the repetition would automatically lead to the observed criterion shift, if the false alarm rate is kept constant by the birds.

In relative localization tasks used to determine the MAA, the subject is trained to indicate a switch in stimulus source location. While in an MAA task the templates can be built on the basis of the repeating stimulus, templates must be developed using long-term memory from previous experience in the absolute MRA task in which no standard is presented. In this task only one source presents the sounds and the subject is trained to show a differential response based on the direction of the sound source. In barn owls (Bala et al. 2003) and cats (Martin and Webster 1987), MAA studies resembled the findings of previous studies on absolute localization accuracy (barn owls: Knudsen and Konishi 1979; cats: Casseday and Neff 1973), but MRA and MAA experiments can also lead to different results in the same species. For example, Jenkins and Masterton (1979) determined an MRA of more than 120° for 1 and 2 kHz tones in the pigeon, while Lewald (1987b) found the best pigeon MAA to reach 4°-6° for 250-500 Hz and 4 kHz tones. However, MAA experiments that determine the relative sound localization accuracy should be carried out with special caution to rule out monaural discrimination cues (Klump 2000). In our study, it is unlikely that the starlings made use of monaural cues to localize sounds since we carefully calibrated the loudspeakers by adjusting their transfer functions by digital filtering and roving the level of the stimuli. This can explain that we find no large discrepancies between our results on the starling MAA of 17° for broadband noise and the MRA of a comparable species like the great tit that reaches 21° for broadband noise (Klump et al. 1986). An experiment that determines the MRA in the European starling would allow quantitatively comparing the two paradigms. Besides unwanted monaural cues, MAA and MRA studies can lead to different results based on the number of standard stimulus presentations prior to the test stimulus. In experiments that determine the MRA, one trial comprises only one stimulus, whereas MAA experiments can comprise multiple standard stimulus presentations in each trial. In their study with cats, Moore et al. (2008) found it quite difficult to directly relate absolute and relative measures of sound localization performance.

A free-field experiment with eastern towhees (*Pipilo erythrophthalmus*) failed to find an effect of stimulus repetition on localization accuracy (Nelson and Suthers 2004). The birds flew to the perceived destination of a playback stimulus consisting of recorded or artificial calls. If a bird did not take flight, the stimulus was repeated up to 30 times with an inter-stimulus-interval of 4 s. The reason for this difference remains unclear, but the longer inter-stimulus interval used in the study by Nelson and Suthers (2004) compared to that in the present study using an inter-stimulus-interval of 1 s for 1 s stimuli and of 1.9 s for 100 ms stimuli may explain the difference. Starlings feature an auditory memory persistence of 2–20 s, depending on the temporal and spectral domain of the stimuli and on the individual subject (Zokoll et al. 2007, 2008).

## 6.5.3. Physiological correlates of sound localization accuracy

In the following, we summarize exemplary studies providing results relating to the accuracy of the neural representation of the available binaural cues. Olsen et al. (1989) determined the tuning accuracy for ITDs and IIDs of neurons in the optic tectum in the barn owl. The width for ITD tuning ranged from 18 to 82  $\mu$ s, with a mean of 40  $\mu$ s. If starlings have a similar capability in the neuronal processing of ITDs (at least up to 3 kHz), the calculated ITDs at the starling's MAA are sufficiently large to be useful for the discrimination of sound source location in an MAA experiment. The tuning width for IIDs in the barn owl's optic tectum (Olsen et al. 1989) ranged from 8 to 37 dB and was larger than the calculated IIDs at the starling's MAA. This neuronal IID tuning does not match the IIDs that other bird species can use for lateralization (see above). Combining behavioral with neuronal MAA measurements in the barn owl, however, Bala et al. (2003, 2007) showed nearly identically increasing behavioral and neuronal sound source discrimination performance with an increase in angular sound source separation indicating a good match between physiological and behavioral results. In the barn owl, the ITD tuning of neurons in nucleus laminaris improves with an increase in the number of stimulus repetitions (Christianson and Pena 2006). This resembles the improvement of the starling's sensitivity with an increase in the number of standard stimulus presentations. An increase in the neuronal response to a deviant with repetition of a standard is also commonly found in human Mismatch Negativity studies that reveal change detection in the brain, although a possible N1 bias in the Mismatch Negativity calculation cannot be ruled out (see Horvath et al. 2008). The Mismatch Negativity increases for an increasing perceived spatial difference between the deviant and the standard stimulus through varying ITD (Paavilainen et al. 1989; Nager et al. 2003; Pakarinen et al. 2007) or IID (Paavilainen et al. 1989) or both cues simultaneously (Doeller et al. 2003). Pakarinen et al. (2007) found that the Mismatch

Negativity amplitude predicted the subjects' probability of detecting a change in location, with larger Mismatch Negativity amplitudes and probabilities of correct response for larger ITDs. Mismatch Negativity studies with free-field conditions found either an all-or-none Mismatch Negativity amplitude for spatial deviants (Paavilainen et al. 1989) or an increase in Mismatch Negativity amplitude for a larger spatial difference of standard and deviant stimulus (Deouell et al. 2006; Sonnadara et al. 2006). In conclusion, studies on the physiology of sound localization in barn owls and humans match the behavioral results.

## 6.5.4. CLOSED-LOOP VERSUS OPEN-LOOP LOCALIZATION

Closed-loop experiments with long stimulus durations allow the subjects to orient and therefore correct their responses based on the sensory feedback. In addition, by the orienting response the subjects may increase the size of the interaural difference cues. Therefore, closed-loop experiments may yield better localization thresholds than open-loop experiments with short stimulus durations that allow only an instantaneous localization without additional orientation responses. In our study, we presented stimulus durations of 1 s (closed-loop) and 100 ms (open-loop) for broadband noise and 2 kHz tones. In the closed-loop condition, the starlings could have adjusted their head position to provide them with better binaural cues allowing them to improve the localization accuracy of each of the repeated standard and test stimuli. This may result in a higher probability of detecting a switch in stimulus location. Alternatively, the longer sound duration may provide the bird with more independent estimates of the binaural cues by evaluating these cues using "multiple looks" with a duration corresponding to the binaural integration time (e.g., Wagner 1991). For the noise-type stimuli, the starling's MAA improved by 11.2° with the longer signal duration, while in the 2 kHz tone types the longer stimulus duration lead to an insignificant improvement of only 3.2°. Rich spectral information may represent an essential stimulus property for the starlings to make use of the longer stimulus duration. Studies in the barn owl (Knudsen et al. 1979) as well as in the great horned owl (Bubo virginianus, Beitel 1991) only found marginal differences between closed-loop and open-loop broadband noise localization. The barn owl showed differences between open-loop (stimulus duration 75 ms) and closed-loop (stimulus duration 1 s) localization of up to only 1° for stimulus source locations between -30° and +30° in azimuth, while these increased to 5-8° for locations of -70° and +70° (Knudsen et al. 1979). In the great horned owl, the accuracy of sound localization did not depend on stimulus durations of 100 ms, 300 ms and 1.6 s (Beitel 1991).

This study allows for a comparison of the available physical cues for sound localization in the starling, determined by Klump and Larsen (1992) with the starling's discrimination of sound source locations. The present behavioral experiments show a relatively good MAA in the starling that can be explained by the available physical interaural cues. For low frequencies, the starling can make use of the ITD, for high frequencies IID cues become important for localizing sound sources. Compared to pure tones, broadband noise offers a wide frequency spectrum that leads to richer sound localization cues and therefore to a better MAA in the starlings under closed-loop conditions. Repeating the standard improves the sensitivity in the MAA experiment.

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## 7. EXPERIMENT II: EFFECT OF HEAD TURNS ON THE LOCALIZATION ACCURACY OF SOUNDS IN THE EUROPEAN STARLING (*STURNUS VULGARIS*)

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## 7.1. Abstract

Long signal durations that represent closed-loop conditions permit responses based on the sensory feedback during the presentation of the stimulus, while short stimulus durations that represent open-loop conditions do not allow for directed head turns during signal presentation. A previous study showed that for broadband noise stimuli, the minimum audible angle (MAA) of the European starling (*Sturnus vulgaris*) is smaller under closed-loop compared to open-loop conditions (Feinkohl & Klump, 2013). Head turns represent a possible strategy to improve sound localization cues under closedloop conditions. In this study, we analyze the influence of head turns on the starling MAA for broadband noise and 2 kHz tones under closed-loop and open-loop conditions. The starlings made more head turns under closed-loop conditions compared to open-loop conditions. Under closed-loop conditions, their sensitivity for discriminating sound source positions was best if they turned their head once or more per stimulus presentation. We discuss potential cues generated from head turns under closed-loop conditions.

## 7.2. INTRODUCTION

In birds, tasks like the identification of predators and potential mates rely on sound localization [1]. Due to the bird's small head size, the European starling (Sturnus vulgaris), a songbird species, faces the problem of small binaural cues, the interaural time difference (ITD) and the interaural intensity difference (IID), for localizing sound sources in the azimuthal plane. In this species, the ITD can reach about 109 to 55 µs for 1 to 4 kHz tones, respectively, and the sound pressure level of frontal speaker positions differs from other azimuthal speaker positions by a maximum of about 2 to 11 dB for 1 to 8 kHz tones, respectively [2]. In a sound localization task, starlings should exploit strategies to enlarge cues or generate additional cues for localizing the sound source. In contrast to open-loop conditions that do not allow for responses based on the sensory feedback, long signal durations that represent closed-loop conditions allow head turns while the signal is still present. The starling minimum audible angle (MAA) for broadband noise stimuli improves from 29° under open-loop conditions to 17° under closed-loop conditions [3]. The improvement under closed-loop compared to open-loop conditions is not significant for 2 kHz tones in starlings but shows a similar trend, reaching 24° and 27°, respectively [3]. These results suggest that starling head turns during stimulus presentation improve sound localization accuracy. Most studies in humans that investigated the effect of head movements on sound localization found positive effects on accuracy. For example, Perrett & Noble [4] demonstrated a better azimuthal localization with compared to without moving the head in human subjects. Letowski & Letowski [5] proposed that benefits from head movements in humans require stimulus durations of at least 600-800 ms. A better

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sound localization accuracy under head-free compared to head-fixed conditions has also been found in rhesus monkeys (*Macaca mulatta*) [6]. In the cat, corrective head movements enhance sound localization accuracy under closed-loop conditions [7], and gaze saccades to auditory stimulus sources are more accurate under head-free compared to head-fixed conditions [8].

In minimum resolvable angle experiments with only one active loudspeaker [e.g., 9], subjects face the task of detecting the direction of the sound (i.e., if the single sound source was presented from the left or from the right). Hence, the ITD and IID represent important cues in starlings that increase in magnitude with azimuth in the frontal field [2]. On the other hand, in MAA experiments with two active loudspeakers like the one analyzed here [3], subjects discriminate between the locations of two sound sources, and therefore the internal representation of both sources affects the threshold.

In humans, the frontal region represents the area of highest azimuthal resolution [e.g. 10, 11], and in an azimuthal sound localization task, human head turns can serve to orient this region toward the stimulus source [12]. Frontal localization accuracy is superior to lateral localization accuracy also in other species like ferrets [13,14], cats [10], rats [15] and barn owls (*Tyto alba*) [16]. Similar to human sound localization accuracy under closed-loop conditions through head turns generated to face toward the sound source with the area of highest azimuthal resolution ("strategy of highest resolution"). Another strategy the starlings may exploit to localize sound under closed-loop conditions is to turn the head toward a position that maximizes the binaural cues available ("strategy of maximal cues") and integrate over time across different estimates. The largest ITDs are generated by sound sources at the back of the starling's head, at about  $\pm 160^\circ$  azimuth [2].

To investigate whether head turns affect sound localization accuracy in these species, we analyze videos of starlings performing a MAA task [3]. We discuss the potential cues generated by head turns that the starlings may exploit to improve sound localization accuracy. We expect to find more head turns under closed-loop compared to open-loop conditions, and to show an improvement in sound localization accuracy with more head turns under closed-loop conditions. If the starling's localization accuracy is best in the frontal area and the subjects turn their head toward the stimulus source, this may represent the strategy of highest resolution. If the starlings orient their head away from the stimulus source, they may employ the strategy of maximal cues.

## 7.3. MATERIALS AND METHODS

In this study, we analyze the relation between head turns and sound localization accuracy in starlings performing in a MAA task published in Feinkohl and Klump [3]. The setup and the conditions applied in obtaining the data are briefly summarized.

## 7.3.1. Subjects

Four European starlings participated in this study. They were caught in the wild and kept in individual cages (1.5 m (W)  $\times$  1.0 m (H)  $\times$  0.7 m (D)). Duck-food pellets (Agravis Geflügelfinisher) represented their main food that was restricted so that the birds reached 92–96% of their free-feeding weight during the experiment.

## 7.3.2. Setup

Stimuli were presented through a semicircle of 15 loudspeakers (diameter = 0.65 m; VifaXT25TG30-04, ASE, Germany). The mean loudspeaker transfer function was adjusted by a 256th order FIR filter, and the level differences between the 13 loudspeakers used were adjusted by an additional 2nd order FIR filter for each loudspeaker. The loudspeakers varied in post filtering total level by  $\pm 1.7$  dB for a bandpass noise between 0.5 to 6 kHz and by  $\pm 1.9$  dB for a 2 kHz tone. Within a frequency range of 0.5 to 6 kHz, individual loudspeakers varied in frequency response by up to  $\pm 3.6$  dB. We observed and recorded the experiments with a webcam (QuickCam Pro 9000, Logitech, Switzerland) from a top view at a resolution of 1280 × 720 pixels and a rate of 15 frames per second. An infrared LED mounted in front of the object lens lit synchronized to the presentation of auditory stimuli.

## 7.3.3. Stimuli

We used two stimulus types, broadband noise signals (0.5–6 kHz) and 2 kHz tones, with a duration of 0.1 s and 1 s including 5 ms Hanning ramps. All stimuli were calibrated to 63 dB overall sound pressure level and roved  $\pm$ 3 dB in level.

## 7.3.4. PROCEDURE

In a Go/NoGo paradigm, the starlings were trained to sit on a perch with their head positioned at about the center of the semicircle of loudspeakers and to report perceived changes in stimulus location by jumping off that perch. Each trial consisted

of 1–5 presentations of a standard stimulus that repeated with an onset-to-onset interval of 2 s, and was then replaced by a single test stimulus. In test trials, we varied the angular distance between standard and test stimuli from 12.9° to 90.0° according to the method of constant stimuli. The location of the sources of standard and test stimuli was unpredictable for the birds. The analysis is based on four to six sessions for each bird and for each of the four stimulus types. Averaged across all four stimulus types, the mean sensitivity d' ranged from 0.52 to 2.83 for a spatial separation of standard and test stimulus of 12.9° and 90.0°, respectively.

## 7.3.5. DATA ANALYSIS

Matlab routines allowed us to analyze the head direction for specific frames of the recorded videos. Video Frames had a duration of 67 ms and were not synchronized with stimulus presentation, so the visual information of a 0.1 s stimulus was recorded in 2–3 frames. For stimulus durations of 0.1 s, the frames analyzed comprised the last frame before the start of the stimulus, the first 2-3 frames during the presentation of the stimulus, and the first frame after the ending of the stimulus. For videos of sessions with stimulus durations of 1 s, we analyzed the last frame before the start of the stimulus, the first 6 frames and the tenth frame during the presentation of the stimulus, and the first frame after the end of the stimulus. This pattern allowed identifying all starling head turns during the presentation of short and long stimuli. The Matlab user interface asked to tag the start and the end of the Culmen (i.e., the line connecting the base of the upper mandible's ridge with the tip). If the video frame was too blurry to identify an unambiguous start and end of the Culmen due to fast head turns, we identified the direction of the head turn (left, right, or indeterminable) based on the following frames. Since the birds possibly turned their head prior to departing from their perch in order to orient toward the landing area, all subsequent frames recorded less than 0.1 s before the birds' departure were excluded from the analysis. All head turns >1° were included in the data analysis.

## 7.4. RESULTS

## 7.4.1. HEAD TURNS

MAA experiments measure the sensitivity when discriminating two different sound source positions, so standard and test stimuli both need to be included in an analysis of the effect of head turns on sound localization accuracy. In a first analysis, the total number of head turns in a trial represented a fixed effect in a Generalized Linear Mixed Model ANOVA (GLMM). We included only sensitivities with a sample size of 10 or more for each number of head turns and each stimulus duration. Other fixed effects were

stimulus type and stimulus duration, and the starling sensitivity d' represented the dependent variable. The individual birds were treated as a random effect. We found that the birds did not differ in sensitivity (p > 0.05), indicating no inter-individual differences in perception. The sensitivity was affected by the total number of head turns (p = 0.037,  $F_{(12,127.031)} = 1.927$ ). Sensitivity was also affected by stimulus type (p = 0.006,  $F_{(1,127.033)} = 7.765$ ) and stimulus duration (p = 0.020,  $F_{(1,127.037)} = 5.513$ ). Figure 7.1 shows the effect of head turns on the sensitivity d' under closed-loop and open-loop conditions. Under closed-loop conditions, the sensitivity generally increases with the total number of head turns, whereas under open-loop conditions the total number of head turns has an ambiguous effect.



**Figure 7.1**: Starling sensitivity for discriminating sound source positions in relation to the total number of head turns per trial, under closed-loop and open-loop conditions, pooled over both stimulus types (mean ± SE).

The number of standard stimuli in a trial varied between 1 and 5, so two effects were present that may have affected sensitivity: On the one hand, more head turns were possible with an increase in the number of standard stimuli. On the other hand, the total time of stimulus presentation in a trial increases with an increase in the number of standard stimuli, and localization accuracy may improve if sound is sampled over a longer period of time. To eliminate the sampling effect and obtain a measure of sensitivity independent of the number of standard stimulus presentations, we *Experiment II: Effect of head turns on the localization accuracy of sounds in the European starling (Sturnus vulgaris)* 

calculated the mean number of head turns per stimulus presentation by dividing the total number of head turns in each trial by the number of stimulus presentations in that trial. To analyze the hypothesized sound localization strategies in the starling, a GLMM analyzed the effect of the stimulus condition on the mean number of head turns per stimulus presentation that was the dependent variable in this analysis. The stimulus type and the stimulus duration were treated as fixed effects and the individual birds as a random effect. The individual starlings did not differ in their number of head turns per stimulus presentation (p < 0.001,  $F_{(1,9)} = 715.835$ ), with a mean of 1.7 head turns per stimulus presentation for durations of 1 s and a mean of 0.6 head turns per stimulus presentation for durations of 0.1 s (p < 0.001, t-test). Therefore, the starlings made more head turns under closed-loop than under open-loop conditions.

Another analysis of the hypothesized sound localization strategies in the starling examined the effect of the mean number of head turns per stimulus presentation under closed-loop and open-loop conditions on the starlings' sound localization accuracy. In the GLMM, the starlings' sensitivity d' was treated as the dependent variable and the individual birds as a random effect. Fixed effects were the stimulus type, the stimulus duration and the mean number of head turns per stimulus presentation. We grouped this variable into 0–1, 1–2, and 2 or more head turns in order to allow for the calculation of sensitivities. The individual starlings did not differ in their sensitivity (p > 0.05). Sensitivity was affected by the mean number of head turns per stimulus presentation (p = 0.014,  $F_{(2.32.002)}$  = 4.865) as well as by stimulus duration (p = 0.002,  $F_{(1,32.004)} = 10.901$ ). Also, there was an interaction of the stimulus duration and the mean number of head turns per stimulus presentation (p < 0.001,  $F_{(2,32.002)}$  = 12.818) that is shown in Figure 7.2. In the conditions with a stimulus duration of 1 s, for a mean number of head turns per stimulus presentation of 1–2 and 2 or more, the starling's sensitivity d' reached 2.2 and 1.8, respectively, and was better compared to a mean sensitivity d' of 1.2 for trials with a mean number of starling head turns per stimulus presentation of 0-1 (p < 0.001 and p = 0.004, respectively, t-tests, Bonferroni-corrected). In the conditions with a stimulus duration of 0.1 s, the starling's sound source discrimination was better for a mean number of head turns per stimulus presentation of 0-1 compared to 2 or more, reaching mean sensitivities d' of 1.7 and 0.8, respectively (p = 0.018, t-test, Bonferroni-corrected). These results indicate that the starlings reached best sound localization accuracy with 1 or more head turns per stimulus presentation under closed-loop conditions, whereas under open-loop conditions their sensitivity decreased with an increasing number of head turns.

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**Figure 7.2**: Starling sensitivity for discriminating sound source positions in relation to the mean number of head turns per stimulus presentation in a trial, under closed-loop and open-loop conditions, pooled over both stimulus types (mean ± SE). Asterisks indicate significant differences.

In addition to the previous analysis of the factors influencing the starling sensitivity d' that included head turns during all stimulus presentations in a trial, we specifically focused our analysis on the number of head turns during test stimulus presentation. This allowed us to judge the importance of head turns during test stimulus presentation only. In a GLMM, the total number of head turns during test stimulus presentation represented a fixed effect. Like in the previous analysis, other fixed effects were stimulus type and stimulus duration, the individual birds were treated as a random effect, and the sensitivity d' represented the dependent variable. The individual birds did not differ in sensitivity (p > 0.05). Sensitivity was affected by the number of head turns per test stimulus (p = 0.002,  $F_{2,33} = 7.797$ ) as well as by stimulus type (p = 0.045,  $F_{1,33}$  = 4.327) and stimulus duration (p = 0.001,  $F_{1,33}$  = 26.862). Also, there was an interaction of number of head turns per test stimulus and stimulus duration (p = 0.021,  $F_{2,33} = 4.382$ ) that is shown in Figure 7.3. In the 1 s conditions, the starlings reached best sensitivities with 1 head turn during test stimulus presentation, and post-hoc comparisons revealed a significant difference compared to 2 or more head turns (p = 0.004, t-test, Bonferroni-corrected). For stimulus durations of 0.1 s, sensitivity did not depend on the number of head turns (all pairwise comparisons p > 0.05, t-tests, Bonferroni-corrected). For test stimuli only, the number of head turns did not affect sensitivity except for a decrease in sensitivity when the starlings turned their *Experiment II: Effect of head turns on the localization accuracy of sounds in the European starling (Sturnus vulgaris)* 

head twice or more under closed-loop conditions. Two additional analyses showed that the mean reaction time for jumping off the perch in response to a test stimulus was 675 ms ( $\pm$ 67 ms SE) for closed-loop stimuli and 669 ms ( $\pm$ 67 ms SE) for open-loop stimuli, and under closed-loop conditions the mean number of head turns during test stimuli was smaller than the mean number of head turns per standard stimulus presentation, reaching 1.52 ( $\pm$ 0.03 SE) and 1.81 ( $\pm$ 0.07 SE), respectively (p = 0.002, t-test for paired samples).



**Figure 7.3:** Starling sensitivity for discriminating sound source positions in relation to the number of head turns per test stimulus presentation, under closed-loop and open-loop conditions, pooled over both stimulus types (mean ± SE). Asterisks indicate significant differences.

The two hypothesized sound localization strategies in starlings, the strategy of highest resolution and the strategy of maximal cues, are based on head turns into a specific direction in relation to the sound source. Therefore, we analyzed the direction of the first head turn during the presentation of the test stimulus in relation to the test stimulus position. Either the starlings turned toward the stimulus, away from the stimulus or did not turn during the test stimulus presentation. We excluded trials with an undeterminable direction of a head turn in a test stimulus frame. In a GLMM, the stimulus type, the stimulus duration and the relation of the first turn during the test stimulus were fixed factors, and the individual birds were treated as a random effect. The relative frequency of head turns was the

dependent variable. The three possible directions of the first head turn varied in relative frequency (p < 0.001,  $F_{(2,36)} = 24.858$ ). There was also an interaction between the relative direction of the first head turn and the stimulus duration (p < 0.001,  $F_{(2,36)}$ = 291.966) that is shown in Figure 7.4. Post-hoc analyses showed that in the 1 s condition, the relative frequency of the direction of the first head turn differed between no turn, turn away from the stimulus source and turn toward the stimulus source, reaching 12%, 35% and 52%, respectively (all pairwise comparisons p < 0.001, t-tests, Bonferroni-corrected). In the 0.1 s condition, the birds mostly did not turn rather than turn into either direction (both pairwise comparisons p < 0.001, t-tests, Bonferroni-corrected). There was no difference in the relative frequency of head turns away from or toward the sound source (p > 0.05, t-test, Bonferroni-corrected). To analyze whether the direction of the first head turn in relation to test stimulus position affected the starlings' sensitivity, an additional GLMM treated the starlings' sensitivity as the dependent variable. The direction of the first turn during the test stimulus was treated as a fixed factor, and the individual birds represented a random effect. As shown in Figure 7.5, the direction of the first head turn during test stimulus presentation did not affect the starlings' sensitivity (p > 0.05). These results indicate that the starlings used conditions with a longer stimulus duration to turn their head mostly toward the stimulus source, but this did not improve their sound localization accuracy. Aside from this result, while monitoring the experiments we did not observe head turns in the starlings directed to bring the semicircle of loudspeakers toward their back during signal presentation.

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**Figure 7.4:** Frequency of head turns for the different directions of the first head turn during test stimulus presentation in relation to test stimulus position, under closed-loop and open-loop conditions, pooled over both stimulus types (mean ± SE). Asterisks indicate significant differences.



**Figure 7.5:** Starling sensitivity for discriminating sound source positions in relation to the direction of the first head turn with reference to the position of the test stimulus being presented. Results obtained with closed-loop and open-loop stimuli are pooled over both stimulus types (mean ± SE).

#### 7.4.2. FRONTAL AND LATERAL SOUND SOURCE POSITIONS

The analysis of the direction of the first head turn in relation to the test stimulus position did not provide evidence that the position of the test stimulus source affects the starlings' sensitivity. In order to directly investigate the effect of sound source position on the starlings' sound localization accuracy, we grouped the position of the test stimulus source in relation to the bird's head orientation into azimuthal sectors of 15°. A GLMM treated the starlings' sensitivity as the dependent variable. The azimuthal sector of test stimulus presentation was treated as a fixed effect and the individual birds as a random effect. We only included sectors with a sample size of 10 or more for each bird, stimulus type and stimulus duration, which resulted in an analysis of test stimulus source positions in the frontal azimuthal field of  $-45^{\circ}$  to  $+60^{\circ}$ . The individual birds did not differ in sensitivity (p > 0.05). The sector did not influence the starlings' sensitivity (p > 0.05), indicating that the birds localized the test stimulus source equally well for all positions within  $-45^{\circ}$  to  $+60^{\circ}$  in the frontal azimuthal field (see Figure 7.6). Therefore, these results do not provide evidence that starlings have an area of highest azimuthal resolution, at least for sound sources between  $-45^{\circ}$  and  $+60^{\circ}$ .



**Figure 7.6:** Starling sensitivity for discriminating sound source positions in relation to the azimuthal sector of test stimulus presentation, pooled over both stimulus types and stimulus durations (mean  $\pm$  SE).

## 7.4.3. HEAD ORIENTATION

During the sound localization experiments, we observed that the starlings did not always orient their head directly toward the front (i.e., 0°). We analyzed the starling head orientation in the last frame before the presentation of a test stimulus. Figure 7.7

shows that they oriented toward the right hemifield, with the mean azimuthal head orientation of the four birds reaching  $+1.2^{\circ}$ ,  $+10.3^{\circ}$ ,  $+15.6^{\circ}$  and  $+15.7^{\circ}$ , respectively.



**Figure 7.7:** Normalized starling head orientation prior to test stimulus presentation, grouped into sectors of 5°. The four colors represent the four individuals.

## 7.5. DISCUSSION

#### 7.5.1. HEAD TURNS

Compared to open-loop conditions, the starlings turned their head more often under closed-loop conditions improving their sound localization accuracy. Both sexes in these species display song with durations of up to 50 s [17], so under natural conditions with long stimuli allowing to use closed-loop localization starlings can benefit from head turns, for example while localizing song of a potential mate. Head turns during playback experiments have been connected to the behavioral relevance of the song in female starlings [18].

In the Introduction, we hypothesized two possible strategies the starlings may employ under closed-loop conditions to improve sound localization accuracy. If the birds turned their head to employ the strategy of maximal cues, they would have needed to reach head positions that face 90° away (maximum ITD) or even 160° away (maximum IID) from the sound source. Our results show that in the MAA experiment under closed-loop conditions, the starlings oriented their heads mostly toward the location of the test stimulus that represented a novel sound source position. This finding and the observation that the birds did not turn around on the perch during signal presentation suggests that they did not employ the strategy of maximal cues. If the starlings employed the strategy of highest resolution, they would have turned their head toward a specific position in relation to the sound source, and the position of the test stimulus should have affected the starlings' sensitivity. Our results show that the starlings mostly turned their head toward the test stimulus position under closed-loop conditions. However, they have precise sound localization accuracy over a broad frontal range, and the direction of the head turn during test stimulus presentation did not affect their sensitivity. These results render it unlikely that the starlings employed head turns directed to face the sound source to improve sound localization. Since the starlings did not benefit from positioning the source in a specific direction, there must be another reason for this behavior. Possibly the starlings showed a reflexive orienting response toward the test stimulus. Orienting the eyes toward the location of the sound source represents one of the major benefits from localizing sound [19] and is a behavior present, among other species, in the barn owl [e.g., 16], the saw-wet owl (*Aegolius acadicus*) [20] and chickens [21].

Although we can reject the strategy of highest resolution and the strategy of maximal cues for sound localization in the starlings, our results show a benefit from head turns on sound localization accuracy under closed-loop conditions. In the following, we will discuss potential cues generated by head turns. A turning starling head generates rates of change in ITD and IID that the bird may use for improving the localization of the sound source. The difference between the ITD cues of two sound source positions varies with azimuth in starlings [see Fig. 4 in 2]. For stimuli presented at 0°, the change in ITD can reach about 1 µs per degree for 1 kHz stimuli and about 2 µs per degree for 4 kHz stimuli. These dynamic ITD cues are relatively similar over a broad frontal area. Only for very lateral stimuli the change in ITD decreases, for example at 80° to about 0.2 µs per degree for 1 kHz stimuli and about 0.3 µs per degree for 4 kHz stimuli. Therefore, dynamic ITD cues generated by head turns for discriminating sound source positions are larger in the frontal azimuthal field compared to lateral positions in the starling. The change in IID cues with azimuth deviates from the change in ITD cues with azimuth in starlings. Klump & Larsen [2] measured the difference in sound pressure level at the right ear's meatus of starlings for frequencies of 1 to 8 kHz. For frontal stimuli (-60° to +60° in azimuth), the average change in sound pressure level reached only 0.006 dB per degree for 1 kHz stimuli and only 0.053 dB per degree for 8 kHz stimuli. For stimulus source positions at about -160°, i.e. at the back of the head, the change in sound pressure level reached up to about 0.2 dB per degree and therefore provided much larger IID cues [see Fig. 1 in 2]. Since we found starling head turns to be mostly directed toward the stimulus source, they may not only serve to generate these dynamic ITD and IID cues, but to maximize the rate of change in ITD. The reason for a lack of an effect of the direction of the head turn in relation to the stimulus position may be related to similar rates of change in ITD over a broad frontal area, encompassing about 60° in azimuth [see Fig. 4 in 2]. Besides generating dynamic binaural cues, starling head turns during closed-loop sound localization also may serve to reach additional static head positions that differ in orientation in relation to the

sound source position. Possibly, the starling brain processes the neuronal responses as independent samples of one sound source position, thereby enhancing the sound localization accuracy.

Compared to static head positions, the processing requirements for localizing a static sound source become much more complex in dynamic head turn conditions. The brain must process the interplay of information from the motor system, proprioception and the auditory system [e.g., 22, 23], and motor commands can mislead the spatial perception in humans [24]. Another challenge is a stable representation of the sound during head turns [25]. In addition, the spatial information can be smeared: Binaural processing in humans features windows of temporal integration, with the window duration ranging from a few ms to a few hundred ms depending on the paradigm [for an overview, see 26]. Taken together, the neuronal processing requirements for localizing static sound sources during head turns are substantial. Our study shows that starlings use head turns to improve sound localization accuracy under closed-loop conditions, indicating that auditory stimulus processing in the starling brain copes with these challenges. Based on a computational model on sensorimotor learning, Aytekin et al. [23] proposed that animals can learn the auditory map of space through active movements.

The starlings rarely turned their head under open-loop conditions, and these head turns probably were not related to the auditory stimulus. Barn owls show mean headturn latencies to novel sound sources of about 100 ms while sitting on a perch [16,27] to about 180 ms during flight [28]. In a sound localization study, Eastern Towhees (Pipilo erythrophthalmus) rarely moved their head during the presentation of a stimulus with a duration of 164 ms [29], and in line with our results on open-loop sound localization in the starling, the authors reported that the probability of correct response did not improve with the presence of head turns. Exemplary for other nonavian species, ferrets orient their head in sound localization tasks after about 200 ms [13,14], and rhesus monkeys show head-turn latencies during sound localization after roughly 150 ms [6]. In humans, the mean reaction time for contracting a neck muscle when presented with sound is 115 ms [30] and is therefore higher by a factor of 1.4 to 2 compared to startle stimuli that evoke neck muscular activations after 55-83 ms [31]. In the starling, the mean auditory startle latency for a sound pressure level of 120 dB reaches 81 ms [32], and assuming a factor for active orientation similar to that in humans, we expect that an active orientation will exceed a duration of 100 ms. In summary, it is likely that stimuli with a duration of 0.1 s terminated before a motor command shaped by sensory feedback could move the starling head.

In the analysis including all stimuli in a trial, sensitivity improved with head turns under closed-loop conditions, while this effect was not present in the analysis of test stimuli only. These results underline the importance of standard stimuli in the MAA task, a finding in line with the observed increase in sensitivity with an increase in the number
of standard stimuli [3]. Repetitions of standard stimuli probably improved the internal template of the standard stimulus location [3]. Possibly, the majority of test stimuli offered salient localization cues to discriminate the sound source location from the standard stimulus location, rendering it unnecessary for the birds to turn the head for maximizing localization performance for closed-loop stimuli. This is in line with the mean reaction time in closed-loop stimulation being lower than the total duration of the test stimulus, and the lower mean number of head turns observed during closedloop test stimulus presentation compared to the mean number of head turns per standard stimulus presentation. Feinkohl and Klump [3] described the starling MAA to be better under closed-loop compared to open-loop conditions for broadband noise stimuli, while the improvement for 2 kHz tones was not significant. In this study, we did not find an effect of stimulus type on the mean number of head turns per stimulus presentation, and no effect of the interaction of stimulus type and mean number of head turns per stimulus presentation on sound localization accuracy. The difference between the large effect of stimulus duration for broadband noise stimuli and the small effect of stimulus duration for 2 kHz tones on the starling MAA may rely on factors other than head turns. For example, the build-up of a spatial representation of the sound source may require sufficiently long stimulus durations [5]. Pollack and Rose [33] found improvements in accuracy with longer stimulus durations despite an absence of head turns in humans, and similar effects have been described in cats [8].

### 7.5.2. Head orientation

In our MAA experiments with the starling, the mean head orientation of three of the four subjects at the beginning of the test stimulus was biased toward the right, similar to results from a 2AFC study on sound localization accuracy in Southern Towhees [29]. It is unlikely that the starlings used such a head orientation to improve sound localization cues. We carefully calibrated the setup, and the sensitivity of the starlings did not depend on the position of the test stimulus source over a broad frontal range. Therefore, there must be other reasons for the bias in head orientation in the starlings.

The lateralization of brain functions allows the hemispheres to simultaneously perform separate tasks [34,35] and possibly can explain the head orientation in the starlings. Lateralization is a "fundamental principle of nervous system organization" [36] and has been found in a variety of classes, including many bird species. Although neuronal lateralization in starlings has been found in the auditory domain for starling song and other stimulus types [37–39], there is no evidence for a lateralization of binaural localization processing. In the visual domain, on the other hand, Schaafsma et al. [40] reported that many birds show lateralization in visually guided behaviors, motor patterns, and cognitive functions. Also, bird species often show head turns to monocularly view stimuli with the stimulus type affecting eye preference [41]. As an

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example for visual object discrimination, feeding responses are biased toward the right side in many birds, including songbirds [42]. In contrast, the European starling was found to be better and learn faster in a visual discrimination task with the left eye than with the right eye [43], a finding in line with more abundant single cone receptors in the left than in the right retina in these species [44]. Although starlings showed no direct lateralization in a visual cue detection task, the transfer of the task was better from the left to the right eye than vice versa [45]. In addition, starlings use monocular vision to observe distant points [46]. Therefore, a possible explanation for the mean starling head orientation toward the right in our experiments may be a general tendency to orient toward the stimulus types in our experiments with the left eye.

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# 8. EXPERIMENT III: AZIMUTHAL SOUND LOCALIZATION IN THE EUROPEAN STARLING (*STURNUS VULGARIS*): III. COMPARISON OF SOUND LOCALIZATION MEASURES

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# 8.1. Abstract

Sound localization studies employed two types of tasks: absolute tasks that measured the localization of the incidence angle of a single sound and relative tasks that measured the localization of the incidence angle of a sound relative to the incidence angle of another sound from a different source. The present study investigates the localization of single sounds in the European starling (Sturnus vulgaris) with a left/right discrimination paradigm. Localization thresholds of 8-12 degrees determined in starlings using this paradigm were much lower than the minimum audible angle thresholds determined in a previous study with the same individuals. The traditional concept of sound localization classifies the present experiment as an absolute localization. However, we propose that the present experiment measured localization of the incidence angle of the sound relative to a non-acoustic spatial frame of reference. We discuss how the properties of the setup can determine if presentation of single sounds in a left/right discrimination paradigm comprises an absolute localization task rather than a localization task relative to a non-acoustic reference. Furthermore, the analysis methods employed may lead to quite different threshold estimates for the same data, especially in case of a response bias in left/right discrimination.

# 8.2. INTRODUCTION

Studies on sound localization have commonly been assigned to two basic types of task: absolute and relative (e.g., Klump, 2000; Moss and Carr, 2012). Absolute tasks require subjects to identify the absolute incidence angle of a single sound source (e.g., Carlile et al., 1997; Makous and Middlebrooks, 1990). Relative tasks require subjects to localize a sound source with reference to the incidence angle of another sound source (e.g., Mills, 1958; Perrott and Saberi, 1990). It has been proposed that the results from the two types of tasks represent different measures of sound localization. Tasks on the identification of the absolute angle of sound incidence measure accuracy and precision that correspond to constant and random errors in sound localization, respectively (e.g., Heffner et al., 2005; Letowski and Letowski, 2012; Moore et al., 2008). Absolute tasks therefore provide information on constant biases in internal space maps and on the variance in the internal spatial representation of sound sources. Tasks evaluating the localization of sound sources relative to other sound sources have measured the Minimum Audible Angle (MAA) that is also referred to as acuity (e.g., Heffner et al., 2005; Moore et al., 2008). These types of relative tasks provide information on how well the auditory system can separate the internal spatial representations of the angles of two sound sources. Correspondingly, acuity is often assumed to be related to precision, although some evidence suggests that separate processing mechanisms may underlie these measures (for review, see Moore et al., 2008). Only studies from few

species allow directly comparing results obtained in absolute and relative sound localization tasks (e.g., barn owl: Bala et al., 2003; Knudsen et al., 1979; cat: May, 2000; human: Recanzone et al., 1998).

The goal of the present experiment was to obtain data for such a comparison in a nonspecialized bird species, the European starling (Sturnus vulgaris), by determining the birds' performance in a left/right discrimination of sound source location and comparing these results with data from a previous MAA experiment in the same individuals. Since in the left/right discrimination task a single sound from one source is presented in each trial, the traditional classification of sound localization tasks would identify this task as an absolute task. However, in analyzing the results it became clear that the present experiment required localization relative to the space coordinates of the setup that can provide a non-acoustic reference, e.g. developed on the basis of visual cues. This challenges the traditional view that all sound localization paradigms with single sound sources correspond to an absolute type of task. Here we discuss in which circumstances left/right discrimination paradigms with a single stimulus represent a relative sound localization task rather than an absolute task and what the implications are for analyzing data from such studies. We evaluate two analysis methods for left/right discrimination tasks and compare their implications. Finally, we relate the results from the present study to those of previous MAA measurements obtained with the same stimuli and in the same individuals.

# 8.3. MATERIALS AND METHODS

The setup and stimulus conditions in this study were similar to those in the previously published study on the starling MAA (Feinkohl and Klump, 2013). Identical materials and methods are briefly summarized.

# 8.3.1. Subjects

The behavioral experiments were conducted with the same four individual European starlings that participated in the previously published MAA study. The birds were kept in individual cages (1.5 m (W) x 1.0 m (H) x 0.7 m (D)) and fed mainly duck-food pellets (Agravis Geflügelfinisher). By restricting food that was provided in the evenings after the experimental sessions had finished, we kept the birds at 87-91 % of their free-feeding weight. To be transported from their cages to the test cage in the adjacent room, the starlings voluntarily entered a wire cage (0.2 m W x 0.2 m H x 0.3 m D). The care and treatment of the birds were in accordance with the procedures of animal experimentation approved by the Niedersächsisches Landesamt für Verbraucherschutz

und Lebensmittelsicherheit, Germany and in accordance with EU Directive 2010/63/EU.

### 8.3.2. Setup

A semicircular array of 15 loudspeakers (Vifa XT25TG30-04, ASE, Germany) surrounded the experimental cage and was shielded from the birds' view by an acoustically transparent but optically opaque cloth. When sitting on the rear waiting perch, the head of the bird was positioned in the center point of the semicircle. A Linux-operated computer controlled the experiment. Two external soundcards (Hammerfall DSP Multiface II, RME, Germany) connected to two sound amplifiers (RMB-1048, Rotel, Japan) controlled the central 9 loudspeakers of the semicircle that presented the stimuli. The angle of sound incidence from adjacent loudspeakers differed by 12.9° (Figure 8.1). A camcorder (Legria HFM56, Canon, Japan) with a resolution of 1920x1080 pixels recorded the bird's head position in the experimental sessions from a top view at a rate of 25 frames per second. 90 small LEDs (LEDlight flex 14 50403215, Barthelme, Germany) and an additional LED (Paulmann, Germany) lit the chamber. A reward light (HighPower LED Spot, Lumitronix, Germany) lit in case of correct responses. A seven-segment display (SA08-11SRWA, Kinbright, Taiwan) attached to the side of the test cage being shielded from the bird's view provided the video recordings with information about the stimulus onset and the bird's response. A light barrier at the rear perch allowed monitoring the bird on the waiting position. Two front perches equipped with light barriers, one at the front left and one at the front right, allowed recording the bird's left/right response. Each of the two front perches allowed access to a custom-built automatic feeder delivering mealworms, respectively.

### 8.3.3. Stimuli

The stimulus types comprised open-loop (i.e., the stimulus terminated before the bird could initiate stimulus-guided movements) 0.1 s broadband noise signals (0.5–6 kHz) and open-loop 0.1 s tones (1, 2 and 4 kHz) that included Hanning ramps of 5 ms. The order of stimulus types tested was randomized for each bird. All stimuli were calibrated to 63 dB SPL and roved  $\pm 3$  dB in level to rule out loudspeaker characteristics as a cue for sound source position. Individual calibration of each loudspeaker determined coefficients used to generate a 256<sup>th</sup> order FIR filter that adjusted the mean loudspeaker spectrum and an additional 2<sup>nd</sup> order FIR filter for each of the 9 loudspeakers that matched the level between loudspeakers. The total level (post filtering) varied between loudspeakers by  $\pm 1.0$  dB for broadband noise ranging between 0.5 and 6 kHz. At 1, 2 and 4 kHz, the loudspeakers varied by  $\pm 1.4$ ,  $\pm 2.4$  and

 $\pm$ 1.9 dB, respectively. The frequency response of individual loudspeakers within the frequency range from 0.5 to 6 kHz varied by up to  $\pm$ 3.9 dB.

# 8.3.4. PROCEDURE

The birds were trained to sit on the rear perch (Figure 8.1). After a waiting period of between 6 and 9 s, a single stimulus was presented at a range of azimuths between - 51.4° and +51.4° using the method of constant stimuli (step size 12.9°). We also presented stimuli from 0° azimuth to obtain responses for a stimulus position indicating only a response bias. In a 2AFC (two-alternative forced choice) left/right discrimination task, the birds were trained to leave the rear perch within the first 1.5 s after stimulus presentation, and jump onto the left or right front perch corresponding to the direction of sound incidence within 1.5 s from leaving the rear perch. The starlings usually jumped from the rear perch directly onto one of the two front perches. Correct responses always resulted in activation of the reward light, and with a probability of 80% in access to a small cooked mealworm (*Tenebrio molitor*, Zoo Med's Can O' Mini Mealies, USA) from the feeder at to the side from which the signal was played. Leaving the rear perch outside of the report phase, responses to the wrong side or misses switched off the chamber light for 5 s. For stimuli presented at 0° any directional response was rewarded.

The previous MAA experiment employed a Go/NoGo paradigm. In the training sessions for the present experiment, the birds quickly adapted to the 2AFC paradigm. In a total of three sessions during the training, probabilistic paradigms that presented targets from one direction more often than from the other untrained biases in the birds to respond to one side more often than to the other side.

Each session comprised 100 trials. After 10 warm-up trials with the stimuli being presented from the sound sources with the largest angular separation from the position at 0° azimuth, 90 trials consisted of a random combination of blocks of ten trials in which each loudspeaker was activated once. A session typically lasted for about 30 min. We allowed each starling a minimum break of one hour between testing and conducted up to four sessions per day and individual. Data analysis based on 3 sessions for each stimulus type and bird.

# 8.3.5. DATA ANALYSIS

One method of analyzing responses in left/right discrimination paradigms with a single stimulus relies on psychometric functions (PMF) that relate the probability of correct responses to the angular separation between pairs of loudspeakers (e.g., Carney et al., 2011; Gatehouse and Shelton, 1978; Heffner and Heffner, 1984, 1992a, 1988a, 1988b,

1982; Heffner and Masterton, 1980; Maier and Klump, 2006; Nelson and Suthers, 2004; Park and Dooling, 1991; Parsons et al., 1999), as illustrated in Figure 8.2a. In the following, this analysis method is termed "loudspeaker pair method" (LPM). Another analysis method relies on PMFs that relate the probability of a directional response to one side (e.g., to the right) to the absolute azimuthal position of the sound source (e.g., Bodson et al., 2006; see also Keating et al., 2013), as illustrated in Figure 8.2b. In the following, this analysis method is termed "absolute loudspeaker position method" (ALPM). To quantify how the LPM and ALPM affect thresholds measured in left/right discrimination paradigms, the data on sound localization in the starling were analyzed with both methods. Since the ALPM analysis set criteria for including sessions, we will first provide details on the ALPM and afterwards describe the LPM.



**Figure 8.1:** Experimental setup and examples for the angular separations used in in the two analysis methods. At trial start the bird sat on the rear perch (a). After a waiting period, a single stimulus was presented from one of the loudspeakers (b) that were shielded from the starlings' view by an opaque cloth (c). The bird was trained to leave the waiting perch and jump on the front perch (d) corresponding to the side from which the stimulus was presented. Food rewards were provided by a feeder (e) at each front perch. The LPM analysis is based the on the angular separation between pairs of loudspeakers (example for the angular separation of one pair indicated by (f)). The ALPM analysis is based on the angular separation of the sound source position from 0° (examples for two angular separations indicated by (g)).

### Analysis with the absolute loudspeaker position method (ALPM)

In the ALPM analysis, a logistic fit (see Lam et al., 1996) of the probability for a response to the right in relation to the absolute position of each speaker represented

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the PMF for each stimulus type and bird. Criteria for valid sessions were chosen similarly to those applied in a study of the Mongolian Gerbil (*Meriones unguiculatus*) by Maier and Klump (2006). A session was included in the analysis if the bird showed a correct directional response to at least 80% of the stimuli from the largest azimuthal angles and showed any directional response (correct or incorrect) in at least 75% of all trials, otherwise the session was discarded. In the three sessions combined for a threshold estimate, the birds had to show a directional response in at least 20 of the 30 trials presenting stimuli from each speaker. In the further analysis, trials with failures to leave the waiting perch in time were discarded from the dataset. For sound sources with the largest angular separation from 0° azimuth, directional responses were not always correct. Thus, we did not restrict the fitted PMF to the minimum and maximum probability of a response to the right of 0 and 1, respectively, but allowed these values to be adapted by the fit. The quality of the fitted PMF needed to reach an R<sup>2</sup> of at least 0.95. If three sessions combined did not fulfill the criteria, we discarded the data from the first session and the bird conducted a fourth session.

The ALPM analysis provides two measures: the directional response bias and the sound localization sensitivity. The directional response bias is defined as the angular separation between 0° and the angle corresponding to the center of the PMF, i.e., representing the angle of the mean of the minimum and maximum of the PMF. The sound localization sensitivity corresponds to the steepness of the PMF, with greater sensitivity being characterized with a steeper PMF. In this study, thresholds are defined as the angular separation between the center of the PMF and the angular position where the PMF deviates in response rate to one side by 0.26 (the symmetry of the PMF would result in identical angular separations between the center of the PMF and 26% more or 26% less responses to the right). In 2AFC experiments analyzed with Signal Detection Theory, a probability for a correct response 26% larger than chance performance corresponds to a d' of 1.0. This threshold criterion is identical to the criterion in the LPM analysis and to the criterion used to calculate the starling MAA in a previous study (Feinkohl and Klump, 2013).

### Analysis with the loudspeaker pair method (LPM)

The LPM analysis relates the mean probability for a correct response for each pair of sound sources, i.e., loudspeakers with an identical absolute angular separation to the position at 0° azimuth, to the angular separation of this pair of sound sources. We used the same valid sessions as in the ALPM analysis. At 0° azimuth responses were ignored and the value of the PMF set to a chance performance of 50%. For each stimulus type and individual bird, linear interpolations of the probabilities for a response allowed to calculate thresholds as the angular position at 76% correct responses, which corresponds to a d' of 1.0. This threshold criterion is identical to the criterion in the

ALPM analysis and to the criterion used to calculate the starling MAA in a previous study (Feinkohl and Klump, 2013).

### Head orientation

In humans, head-to-trunk position can affect the internal coordinate system. For example, the subjective auditory median plane of the head can be shifted towards the head direction (e.g., Lewald and Ehrenstein, 1998; Lewald et al., 2000; Schicke et al., 2002). Similar effects of head-to-trunk position on changes in the internal spatial coordinate system in starlings may result in a directional response bias towards the head direction. To analyze the effect of head direction on the directional response bias, a custom-written Matlab code analyzed videos of all sessions and allowed to manually determine the starling's head direction at stimulus onset in each trial. Trials were excluded from the analysis in case of ambiguous head directions, for example those being due to fast head movements that resulted in video frames with blurred images, or if the seven-segment display was occluded from the video image.

## 8.3.6. MAA CONTROL EXPERIMENT

The same four individual starlings had participated in a previously published experiment on the MAA (Feinkohl and Klump, 2013) and subsequently in the present experiment. To control for training effects, we repeated the previous MAA experiment with 0.1 s broadband noise after the individual starlings finished all sessions of the present left/right discrimination experiment.

### 8.4. RESULTS

Before a threshold was calculated, mostly 4 sessions were conducted. The ALPM analysis resulted in a sigmoidal fit of three sessions combined that did not reach a R<sup>2</sup> of 0.95 only once, so an additional session was conducted. In the sessions included in the analysis, the birds missed to respond in only 3% of all trials, and these trials were excluded from further analysis. The starlings reached a mean correct directional response of 99% for sound sources with the largest angular separation from the position at 0° azimuth. This indicates that the birds reliably solved the sound localization task.

Figure 8.2 shows the PMFs resulting from analyses with the LPM and the ALPM for all subjects and stimulus types. The mean directional response bias determined with the ALPM analysis was +0.5° (±7.0° SD), and the mean absolute directional response bias

reached 4.8° (±5.0° SD). The PMFs determined with the LPM and the ALPM analysis for each bird and stimulus type resulted in the thresholds shown in Figure 8.3. The analysis with the LPM resulted in mean thresholds of 28.6° for 1 kHz, 31.7° for 2 kHz, 29.0° for 4 kHz and 24.6° for broadband noise stimuli. The analysis with the ALPM resulted in mean thresholds of 12.0° for 1 kHz, 7.9° for 2 kHz, 7.9° for 4 kHz and 8.3° for broadband noise stimuli. To eliminate the difference in relating performance to azimuthal angle between the LPM and the ALPM analysis ("factor 2 effect"), Figure 8.3 also shows doubled ALPM thresholds.

# 8.4.1. EFFECT OF ANALYSIS METHOD ON THRESHOLD

We analyzed the factors influencing thresholds with a Generalized Linear Mixed Model (GLMM) ANOVA. The determined threshold was the dependent variable in the analysis. The birds were included as a random effect, fixed effects were the stimulus type and the analysis method (LPM or ALPM). The starlings did not differ in their sensitivity (p>0.05). Only the analysis method had a significant influence on thresholds  $(p<0.001, F_{(1,24)}=140.908)$ . A post-hoc analysis showed that the ALPM analysis resulted in lower thresholds than the LPM (p<0.001, t test). The two-way interaction of analysis method and stimulus type did not reach significance (p>0.05). These results indicate that the analysis method affected thresholds, while thresholds did not differ between stimulus types. To analyze whether only the factor 2 effect accounts for this difference in thresholds between the two analysis methods, we repeated the GLMM ANOVA with doubled ALPM thresholds compared to the previous GLMM ANOVA. All results remained identical to the previous GLMM ANOVA, with the exception of a lower Fvalue for the significant effect of analysis method on thresholds (p<0.001,  $F_{(1,24)}$ =35.901). This indicates that besides the factor 2 effect, other factors affect the difference in LPM and ALPM thresholds.

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**Figure 8.2:** Psychometric functions for all birds and all stimulus types, determined with the LPM and the ALPM analysis. The colors represent the individual subjects. a) The LPM relates the mean probability for a correct response to angular separations of loudspeaker pairs. Linear interpolation allows calculating the threshold as the angular separation between 0° and the angular position at a mean probability for a correct response of 0.76. This corresponds to a d' threshold of 1.0. Note that chance performance is set to a probability for a correct response of 0.5. b) The ALPM analysis relates the probability for a response to one side to absolute azimuthal loudspeaker positions and fits sensitivity with a logistic function (all  $R^2 \ge 0.95$ ). Thresholds are defined as the angular separation between the angular position at the center of the PMF and the angular position at a probability for a response to one side 0.26 higher or lower than the center of the PMF. This corresponds to a d' threshold of 1.0.

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**Figure 8.3:** Thresholds for the four stimulus types (means ±SE), determined with the LPM and the ALPM analysis. We also included doubled ALPM thresholds to show that the difference between LPM and ALPM thresholds cannot only be explained by the factor 2 effect, i.e. the difference in relating responses to azimuthal angle.

#### 8.4.2. EFFECT OF RESPONSE BIAS ON THRESHOLD

The ALPM analysis accounts for a directional response bias, whereas the LPM analysis does not. The following analyses will show whether, besides the factor 2 effect, the directional response bias represents a source for the differences in thresholds determined with the two analysis methods. The directional response biases for each bird and stimulus type included in the analyses below are based on the ALPM analysis. Thresholds determined with the LPM analysis correlated with absolute directional response bias (Spearman rank correlation coefficient rs = 0.55, p=0.014). Since the ALPM analysis accounts for directional response bias, ALPM thresholds represent a reference to reduce the effect of the individual threshold on the correlation between absolute directional response bias. The size of the difference, 100%) in relation to absolute directional response bias. The size of the difference correlated with the absolute directional response bias. The size of the difference correlated with the absolute directional response bias. The size of the difference correlated with the absolute directional response bias (Spearman rank correlation coefficient rs = 0.80, p<0.001). This indicates that an increase in absolute directional response bias increased the difference between thresholds determined with the LPM analysis.

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**Figure 8.4:** Difference between LPM and ALPM thresholds in relation to absolute directional response bias, for each bird and stimulus type.

The video analysis showed mean head directions of the four starlings at the beginning of a stimulus of -12.8° ( $\pm$ 32.5° SD), +19.9° ( $\pm$ 14.6° SD), +15.9° ( $\pm$ 22.3° SD) and +25.0° ( $\pm$ 20.9° SD), respectively. Figure 8.5 shows a scatterplot of the mean head direction for each subject and stimulus type in relation to the directional response bias. The pattern does not indicate that response direction was biased by head direction. This is confirmed by a GLMM ANOVA analyzing factors influencing directional response bias that was the dependent variable in the analysis. Subjects were included as a random effect, fixed effects were the stimulus type and the mean head direction. Directional response bias did not differ between subjects (p>0.05). Response bias was not affected by stimulus types, head direction or a two-way interaction of these factors (p>0.05, respectively).



directional responsebias determined with the ALPM [°]

**Figure 8.5:** Mean head direction at the beginning of the stimulus for each subject and stimulus type in relation to the directional response bias determined with the ALPM. The colors represent the individuals.

## 8.4.3. Comparison with MAA thresholds

In a previously published experiment (Feinkohl and Klump, 2013), we reported MAA thresholds for the same four birds. Stimulus types included 2 kHz tones and broadband noise with a duration of 0.1 s. The following analysis compares thresholds from the present study and MAA thresholds for these two stimulus types. In a GLMM ANOVA, the sound localization thresholds were the dependent variable. The birds represented a random effect, fixed effects were the stimulus type and the paradigm (MAA, thresholds determined with the LPM analysis, thresholds determined with the ALPM analysis). Thresholds did not differ between birds (p>0.05), and only the paradigm affected the thresholds (p<0.001, F(2.18)=27.293). Thresholds determined with the ALPM analysis were lower than those determined with the LPM analysis (p<0.001, t test, Bonferroni-corrected, see 3.1 above). Thresholds determined with the ALPM analysis were also lower than the MAA thresholds (p<0.001, t test, Bonferronicorrected). Thresholds determined with the LPM analysis did not differ from MAA thresholds (p>0.05, t test, Bonferroni-corrected). These results show that starling thresholds determined with the LPM analysis are similar to MAA thresholds, whereas thresholds determined with the ALPM analysis are better than MAA thresholds.

The MAA control experiment resulted in a mean MAA threshold of  $29.0^{\circ}$  (±0.9° SE) for 0.1 s broadband noise. In the previous MAA experiment (Feinkohl and Klump, 2013), the starlings reached a mean threshold of  $28.6^{\circ}$  (±1.1° SE) for this stimulus type. This negligible difference did not reach significance (p>0.05, t test for paired samples), which indicates that the starlings' extended training in sound localization tasks did not affect results.

### 8.5. DISCUSSION

Absolute localization and localization relative to another sound source represent the two types of sound localization task that are traditionally distinguished (e.g., Klump, 2000; Moss and Carr, 2012), and each provides unique information on the processing of sound source angle. Studies on the identification of the absolute incidence angle of sound measure accuracy and precision, whereas studies on the localization of the incidence angle of sound relative to the incidence angle of another sound source measure acuity (e.g., Heffner et al., 2005; Moore et al., 2008). It is still under debate how results from these two types of localization task correspond (for review, see Moore et al., 2008). In a previous experiment, we measured acuity in the European starling by determining the MAA (Feinkohl and Klump, 2013). To compare this measure of localization relative to another sound source with absolute localization in the same setup, we conducted a left/right discrimination

experiment with single incidence angles of sound that is commonly considered to measure absolute localization (e.g., Klump, 2000; Moss and Carr, 2012). However, during the analysis we noticed that this type of task may be solved by localization relative to a non-acoustic spatial frame of reference that represents the transition angle between left and right sound source positions. This represents a relative type of localization task involving more than the auditory modality. Therefore, not all sound localization experiments with a single stimulus correspond to absolute sound localization tasks.

In the following, we will first discuss how the experimental setup may influence the type of task in left/right discrimination paradigms with a single stimulus. The type of task determines which of two analysis methods, the LPM and the ALPM, should be employed to analyze the data. Based on the data from the present experiment with European starlings, we demonstrate large differences between thresholds analyzed with the two methods and identify the major causes. Finally, we will compare thresholds from the present study to localization acuity measured previously in the European starling in a MAA experiment (Feinkohl and Klump, 2013).

# **8.5.1.** How to analyze data from left/right discrimination experiments with a single stimulus: Type of task and choice of analysis method

Sound localization studies in animals often employ a left/right discrimination paradigm that requires subjects to determine whether a single sound was presented from a source to the left or to the right of 0° azimuth (e.g., Bodson et al., 2006; Carney et al., 2011; Gatehouse and Shelton, 1978; Heffner and Heffner, 1984, 1992a, 1988a, 1988b, 1982; Heffner and Masterton, 1980; Maier and Klump, 2006; Nelson and Suthers, 2004; Park and Dooling, 1991; Parsons et al., 1999; Terhune, 1974). Since only one stimulus is broadcast, this type of task is commonly considered to be absolute and reported as the Minimum Resolvable Angle (MRA) (e.g., Klump, 2000; Moss and Carr, 2012). However, only if subjects identify the angle of the sound source that presented the single stimulus, the left/right discrimination experiment represents an absolute task. If directional responses are based on the localization of the sound source relative to a non-acoustic spatial frame of reference, thresholds are measured in a relative type of task that requires sound localization relative to non-acoustic references. Two properties define whether subjects can identify the absolute position of the single sound source with a left/right response: The number of sound source pairs and the visibility of sound sources. In the following, we will discuss how these properties affect the type of sound localization task and how the type of task defines whether the LPM or the ALPM should be used to analyze the data.

### One pair of visible sound sources

Visual spatial resolution is superior to the auditory spatial resolution in many animals (e.g., see Heffner and Heffner, 1992b), and visual acuity thresholds are much lower than one degree even in small non-specialized bird species (e.g., Harmening and Nikolay, 2009). If one visible pair of sound sources presents the single stimuli in a left/right discrimination paradigm (e.g., Klump et al., 1986), the subject may discriminate the incidence angle of the sound within that pair if it realizes that all stimuli are presented only from the two sound sources. An optimal processing mechanism would employ the reference that is internally represented most precisely, in this case the visually determined angle of the two sound sources. The subject can assign the perceived incidence angle of each sound to one of the two visually determined angles of sound sources and give a corresponding directional response. Thus, the subject would identify the absolute angle of sound incidence and therefore solve an absolute task. However, in constrast to this absolute localization task with the aid of visual cues, a true measure of absolute sound localization lacks the influence of cues from non-acoustic modalities. For example, visual cues in absolute localization tasks can be ruled out by blindfolding subjects or conducting experiments in total darkness (e.g., Carlile et al., 1997).

In contrast, the subject may also solve the left/right discrimination task with single stimuli presented from visible sound sources by comparing the perceived angle of sound incidence to a non-acoustic spatial frame of reference that internally defines the transition angle between left and right. This reference angle may be anywhere, however, a left/right discrimination in reference to a lateral non-acoustic reference angle would lead to more errors compared to a frontal non-acoustic reference angle. A non-acoustic reference angle at 0° azimuth would result in the least errors since it represents the true transition angle between stimuli presented from the left and presented from the right.

Thus, the type of task in left/right discrimination experiments with one visible pair of sound sources depends on the subject's behavioral strategy regarding the reference. This may affect interindividual variance in thresholds since the angular separation between the two sound sources is twice as large as the angular separation between a sound source and a non-acoustic reference angle at 0° azimuth (Figure 8.1). If subjects realize that only the two sound sources present stimuli, optimal processing predicts that left/right responses are based on the visual information about the angle of the sound source.

The type of task in a left/right discrimination experiment defines the method for analyzing data from left/right discrimination paradigms with a single stimulus. The LPM analysis relates the subjects' responses to the angular separation between pairs of loudspeakers that have the same angular separation from 0° azimuth (Figure 8.1). It is

based on the assumption that subjects identify loudspeakers as pairs and discriminate the angle of sound incidence within pairs. A directional response would indicate which visually identified source presented the stimulus and thus represent the absolute identification of the angle of sound incidence. Therefore, data from a left/right discrimination paradigm with a single stimulus should be analyzed with the LPM if it represents an absolute task.

### Invisible or multiple pairs of sound sources

If invisible sound sources (e.g., the present study; Gatehouse and Shelton, 1978) present the stimuli, the subject lacks information about the angles of the sound sources and therefore cannot identify the absolute angle of sound incidence with a left/right response. Rather, the subject's left/right response indicates the perceived angle of sound incidence relative to the internal transition angle between left and right, a non-acoustic reference angle. Thus, left/right discrimination experiments with invisible sound sources represent localization tasks relative to a non-acoustic reference. The ALPM analysis relates the subjects' responses to loudspeaker positions and is based on the assumption that subjects discriminate the perceived angle of sound incidence from the angle at 0° azimuth (Figure 8.1). This corresponds to sound localization relative to a non-acoustic reference, so the ALPM should be used to analyze data from a left/right discrimination experiment with invisible sound sources.

If more than one pair of visible sound sources present stimuli (e.g., Heffner and Heffner, 1984), the left/right discrimination experiment with single stimuli represents a localization task relative to a non-acoustic reference position. Even if the subject unambiguously identifies the sound source that presented the stimulus with the aid of visual cues, it is bound to choose between a response to the left or the right and is therefore unable to report the absolute angle of sound incidence. Rather, the left/right response is based on the perceived incidence angle of sound relative to a non-acoustic reference angle. As described above, the assumptions underlying the ALPM are in line with the localization relative to a non-acoustic reference, so the ALPM is appropriate for analyzing responses. Thus, data from a left/right discrimination paradigm with multiple visible sound source pairs presenting the stimuli should be analyzed with the ALPM.

# 8.5.2. Comparison of thresholds determined with the LPM and the ALPM ANALYSIS

The present study measures directional responses of European starlings in a left/right discrimination experiment for broadband noise and tones and analyzes data with the

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LPM and the ALPM. Although the experiment represents a localization task relative to a non-acoustic reference and data should thus be analyzed only with the ALPM (see above), we also analyzed data with the LPM to point out differences between thresholds determined with the two methods. The ALPM resulted in lower thresholds than the LPM, although both analyses of starling thresholds were based on the same data from the left/right discrimination task and threshold criteria in both analysis methods corresponded to d'=1.0. The following section will provide details on the two major causes for this difference: the method of relating the subject's responses to the azimuthal angle, and the influence of the directional response bias on LPM thresholds.

### Relating the subjects' responses to azimuthal angle

The LPM analysis relates the subjects' responses to the angular separation between pairs of loudspeakers that have the same angular separation from the position at 0° azimuth (Figure 8.1). It is based on the assumption that subjects identify loudspeakers as pairs and discriminate the angle of sound incidence between loudspeaker positions and is based on the assumption that subjects' responses to the loudspeaker positions and is based on the assumption that subjects discriminate the angle of sound incidence relative to a non-acoustic reference angle, for example at 0° azimuth (Figure 8.1). Thus, the azimuthal angles underlying the analysis of the same responses are twice as large in the LPM compared to the ALPM (factor 2 effect). Since in the present study doubled ALPM thresholds are still better than LPM thresholds (see Figure 8.3), the differences in thresholds between the two analysis methods cannot be explained only by the factor 2 effect. A directional bias in the subject's responses represents another major source for the difference in determined thresholds between the LPM and the ALPM analysis.

### The influence of directional response bias on threshold

Many sound localization studies in animals using a left/right discrimination paradigm seek to untrain directional response biases (e.g., Klump et al., 1986; Park and Dooling, 1991), but these cannot be ruled out without analyzing the raw data. Bias in response direction can be evoked through a constant shift in auditory spatial perception resulting for example from asymmetries in the subject's hearing or the listening conditions, or from a general tendency of preferring one response over the other (e.g., Hartmann and Rakerd, 1989; Letowski and Letowski, 2012). The ALPM analysis provides separate measures of sound localization sensitivity and of directional response bias. The steepness of the PMF determines the threshold that is unaffected by an azimuthal angular shift of the PMF, i.e. a directional response bias (see also Hartmann and Rakerd, 1989). Figure 8.6a shows exemplary simulated PMFs with

directional response biases ranging from 0° to 20°. All have the same steepness, thus the ALPM analysis results in the same thresholds for all PMFs irrespective of directional response bias.

In contrast to the ALPM, the LPM analysis does not account for a directional response bias. For each pair of loudspeakers, it calculates the mean probability for a correct response. The simulated PMFs in Figure 8.6a share the same steepness but differ in directional response bias. As discussed above, these result in the same thresholds calculated with the ALPM. For this set of PMFs, Figure 8.6b shows the corresponding mean probability for a correct response for each pair of sound source positions as calculated in the LPM. It illustrates that the mean probability for a correct response for sound source positions with the same angular separation to 0° azimuth decreases with an increase in directional response bias. As an example, the probabilities for a response to the right at sound source positions of -5° and +5° are indicated by horizontal dashed lines in Figure 8.6a for two simulated PMFs with the same steepness and a directional response bias of 0° and 8°, respectively. The corresponding mean probability for a correct response for sound source positions with an angular separation of 5° to the position at 0° azimuth is lower for the PMF with a directional response bias of 8° compared to the PMF with a directional response bias of 0°, as indicated by horizontal dashed lines in Figure 8.6b. Thus, simulated responses show that thresholds determined with the LPM analysis correlate with directional response bias, which results from the averaging of probabilities for a correct response for pairs of sound sources. Results from the present study confirm the increase in LPM thresholds with an increase in absolute directional response bias (Figure 8.4). The present discussion of the effects of response bias on thresholds calculated with the LPM focuses on response bias to the right. Response bias to the left would result in identical effects on thresholds calculated with the LPM.

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**Figure 8.6:** Simulated effect of directional response bias on the mean correct response for sound source positions with the same angular separation to 0° azimuth. Directional response biases affect LPM but not ALPM thresholds. a) Simulated responses with the same steepness and directional response biases ranging from 0° to 20°. All PMFs correspond to a threshold of 5° determined with the ALPM analysis. Vertical dashed lines indicate the position of a pair of loudspeakers at -5° and +5°. For these two sound source positions, horizontal dashed lines indicate the probabilities of response to the right for PMFs with a directional response bias of 0° and 8°, respectively. b) Resulting mean probabilities for a correct response for pairs of sound sources with the same angular separation to 0° azimuth. The horizontal dashed lines show that for a directional response bias of 0°, the mean probability for a correct response remains identical to the probability for a correct response for the two absolute loudspeaker positions. For a directional response bias of 8°, the mean probability for a correct response for the same angular separation of sound source position to 0° azimuth is lower than for a directional response bias of 0°. Thus, an increase in directional response bias decreases the mean probability for a correct response.

Simulated responses and experimental results confirmed that unlike ALPM thresholds, LPM thresholds increase with an increase in directional response bias. Next, we seek to quantify the error in LPM thresholds resulting from a directional response bias. Figure 8.7a shows LPM thresholds determined from simulated responses that result in ALPM thresholds between 5° and 30° and directional response biases ranging between 0° and 40°. As pointed out in the previous paragraph, LPM thresholds increase with an increase in directional response bias. Note that we discounted LPM thresholds in Figure 8.7 by 50% to avoid the factor 2 effect. Based on the difference between LPM and ALPM thresholds shown in Figure 8.7a, Figure 8.7b illustrates that the error in LPM thresholds correlates with directional response bias. The following examples show that response bias may considerably affect sound localization thresholds analyzed with the LPM. ALPM thresholds of 5° and 10° (i.e. LPM thresholds of 10° and 20° due to the factor 2 effect) are well in the range of sound localization thresholds of many species (e.g., Heffner, 1997). For a threshold of 5° determined with the ALPM, a directional response bias of 5° results in an increase in LPM threshold by 30%. With a directional response bias of 10°, this error increases to more than 100%. For a threshold of 10°

determined with the ALPM, the increase in LPM threshold reaches 30% for a directional response bias of 10°.



**Figure 8.7:** Simulated size of the effect of directional response bias on LPM thresholds. We discounted LPM thresholds by 50% to avoid the factor 2 effect. a) Simulated ALPM thresholds ranging between 5° and 30° and directional response biases between 0° and 40° result in LPM thresholds that depend on the size of directional response bias. b) The resulting error in LPM thresholds increases with an increase in directional response bias.

As outlined above, a directional response bias may be due to the head-to-trunk position. Although many sound localization studies in animals with left/right discrimination paradigms control for the animal position relative to the position of the sound source (Heffner and Heffner, 1992b), animal head direction often is not restricted. This is similar to the present study that allowed the starlings to move freely on the rear perch. The starlings mostly directed their head towards the right, which resembles head directions measured in the previous study on the MAA in the same individuals (Feinkohl et al., 2013). In the present study, the bias in directional response was not affected by head direction. This indicates that unrestricted head direction in the present experiment did not introduce biases (but see Feinkohl et al., 2013 for the effect of starling head movements on sound localization under closed-loop conditions).

### 8.5.3. Comparison of relative sound localization thresholds

The task in the present study measured sound localization relative to a non-acoustic reference angle, while MAA studies measure sound localization relative to an acoustic reference angle. MAA thresholds in the same starlings that participated in the present study were measured previously (Feinkohl and Klump, 2013). In the following, we will

compare these to thresholds from the present study and discuss factors that may produce the threshold differences. Only ALPM thresholds will be included in the comparison since this method is most appropriate to analyze data from the present experiment (see above).

A comparison of the two relative thresholds requires stimulus types with the same spectrum and duration in both experiments (Feinkohl and Klump, 2013; Feinkohl et al., 2013). This applies to broadband noise and 2 kHz tones with a duration of 0.1 s. In the present study, these resulted in mean thresholds of 7.9° and 8.3°, respectively. Corresponding mean MAA thresholds in the previous study reached 27.4° and 28.6°, respectively. Thus, for these stimulus types, thresholds in the present study were much lower than MAA thresholds. In a control MAA experiment following the present study, we replicated the mean MAA threshold for 0.1 s broadband noise from the previous study to less than half a degree with the same individuals. This shows that extended training in sound localization tasks did not influence present thresholds and cannot explain differences between the two types of relative thresholds. In the following, we will discuss major possible factors underlying the threshold differences; the comparison using acoustic or non-acoustic frames of reference, and potential differences related to the procedures applied in the two experiments.

### The effect of the sensory modality used for a reference

The differences in sound localization thresholds measured in the two types of relative tasks are probably related to differences in sensory modalities used for a reference. Relative sound localization relies on the distributions of the subjects' internal spatial representations of the angles that are compared (e.g., Moore et al., 2008). The MAA experiment required comparing the incidence angle of the acoustic test stimulus to the incidence angle of preceding acoustic standard stimuli. The present study required comparing the incidence angle of the acoustic test stimulus relative to the angle of a non-acoustic spatial frame of reference. Thus, the type of reference differs between the two relative tasks, and therefore the internal spatial distribution of the reference angle may differ between the two experiments. Signal Detection Theory allows predictions on the discriminability of test and reference angle: Thresholds increase with broader distributions of the internal spatial representation of the reference angle. Since thresholds in the present study were much better than MAA thresholds measured previously, the internal spatial representation of the reference in the MAA experiment is probably less precise than of the reference in the present experiment, which is illustrated in Figure 8.8. Internal distributions overlap significantly for an angular separation close to the spatial resolution of the auditory system (Figure 8.8a). If the non-acoustic reference angle is internally represented more precisely than a sound source at the same angle, it overlaps much less with the internal spatial distribution of test stimulus angle than the internal spatial distribution of the acoustic reference angle in the MAA experiment (Figure 8.8a). Corresponding ROC curves shown in Figure 8.8b predict better performance for spatial discrimination of test stimulus and non-acoustic reference compared to test stimulus and acoustic reference. This corresponds to the difference in thresholds measured in the present experiment and in the MAA experiment. One explanation for a more precise internal representation of the non-acoustic reference angle is an influence of the visual modality. As indicated by other studies on visual acuity in animals outlined above, starling vision is probably at least one order of magnitude more precise compared to auditory acuity measured in the study on the starling MAA (Feinkohl and Klump, 2013). Thus, the visual modality may have provided the non-acoustic reference angle in the present sound localization experiment.



**Figure 8.8:** a) Simulated distributions of the internal spatial representation for the angle of two sound sources in the experiment on the starling MAA and the angle of one sound source and a one non-acoustic reference angle in the present experiment. To illustrate the difference between the two experiments, the angular separation of the two sound sources equals the angular separation of the single sound source and the non-acoustic reference. In the MAA experiment, a test stimulus (dashed distribution) follows a repeated standard stimulus (green solid distribution). The angles of standard and test stimulus differ (dotted vertical lines). The birds were trained to detect the switch in stimulus angle. An angular separation between test and standard stimulus close to the spatial resolution of the auditory system results in significant overlap of the two internal distributions. The present experiment required comparing the internal spatial representation of the angle of the test stimulus (dashed distribution) to the probably more precise internal spatial representation of a non-acoustic reference angle (red solid distribution). b) Resulting ROC curves predict better performance in the present experiment than in the MAA experiment.

### Differences between procedures

The relative type of task in the present study resulted in better thresholds than the relative type of task in the previous MAA study with the same starlings. Besides the difference in precision of the internal representation of acoustic and non-acoustic references discussed above, the difference in thresholds may also have been affected by differences in cognitive demands and strategies employed by the starlings between the 2AFC paradigm in the present study and the Go/NoGo paradigm in the MAA experiment.

The cognitive demands of Go/NoGo tasks that require subjects to report changes in the stimulus are lower than the cognitive demands of 2AFC tasks that force subjects to choose between different stimulus characteristics and hence to classify the stimulus (e.g., Lit, 2009; Walker et al., 2009). In our studies on starling sound localization, this difference in cognitive demands would have predicted better performance in the MAA experiment, probably independent of whether stimuli were salient or in the threshold range. However, we found the opposite difference between thresholds and the starlings reached a probability for a correct response of nearly 1 for the easiest stimuli in the present study. Thus, we conclude that cognitive demands are unlikely to have limited starling performance.

Strategies employed by the starlings may have differed between the two experiments for stimuli presented in the threshold range. In human subjects, Go responses in Go/NoGo experiments can be faster and more accurate than corresponding responses in 2AFC experiments (for review, see Gomez et al., 2007). Shenoy and Yu (2012) demonstrated that if the Go response results in an immediate termination of the trial and the beginning of the next trial, a Bayes-optimal decision strategy avoids the waiting interval that precedes the end of the trial by preferring fast Go responses, a policy the authors termed "strategic impatience". The starlings in the Go/NoGo MAA experiment probably did not develop this strategy since a false alarm delayed the end of the trial for 5 s. However, this may have resulted in a "strategic patience": Since NoGo responses did not result in temporal delay of the next trial, a trade-off between accuracy and speed in the starlings' policy may have resulted in a bias towards the NoGo response for stimuli in the threshold range. In contrast, the present 2AFC experiment negatively reinforced misses with a temporal delay of 5 s. Consequently, the starlings responded to nearly all stimuli presented.

# 8.6. CONCLUSION

Left/right discrimination experiments with a single stimulus in each trial may correspond to localization relative to a non-acoustic spatial frame of reference. Employing the single-stimulus paradigm, sound localization thresholds of European

starlings were found to be much lower than MAA thresholds determined previously in the same individuals. This suggests that the modality used as a reference in the present study was internally represented more precisely than the acoustic reference in the MAA experiment. The ALPM represents an appropriate analysis method in experiments on localization relative to a non-acoustic reference, and it minimizes the influence of bias in directional response on thresholds. Left/right discrimination experiments with a single stimulus may reflect absolute localization thresholds if one pair of visible sound sources present the stimuli. Under these conditions, the commonly used LPM represents an appropriate analysis method. However, a directional response bias may have profound effects on thresholds calculated with the LPM.

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*Experiment III: Azimuthal sound localization in the European starling (Sturnus vulgaris): III. Comparison of sound localization measures* 

Walker, K.M.M., Schnupp, J.W.H., Hart-Schnupp, S.M.B., King, A.J., Bizley, J.K., 2009. Pitch discrimination by ferrets for simple and complex sounds. *J. Acoust. Soc. Am.* 126, 1321–1335.

# 9. EXPERIMENT IV: THE EFFECT OF VELOCITY ON AUDITORY REPRESENTATIONAL MOMENTUM

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# 9.1. Abstract

"Representational Momentum" (RM) is a mislocalization of the endpoint of a moving target in the direction of motion. In vision, RM has been shown to increase with target velocity. In audition, however, the effect of target velocity is unclear. Using a perceptual paradigm with moving broadband noise targets in Virtual Auditory Space resulted in a linear increase in RM from 0.9° to 2.3° for an increase in target velocity from 25°/s to 100°/s. Accounting for the effect of eye position also reduced variance. These results suggest that RM may be the result of similar underlying mechanisms in both modalities.

# 9.2. INTRODUCTION

The localization of moving objects plays an essential role for many species in their interaction with the natural environment. In the visual domain, the perception of a moving target's endpoint tends to be displaced in the direction of motion, a mislocalization effect termed "Representational Momentum" (RM). Over the past 30 years, visual studies have determined a large number of variables influencing RM <sup>1</sup>, and hypothesized several theories underlying this forward displacement <sup>2</sup>. Evidence that RM might also be present in the auditory domain <sup>3</sup> preceded the first findings in the visual domain <sup>4</sup>; however, the handful of studies investigating auditory RM <sup>5-9</sup> have shown varied and conflicting results.

Visual RM has been found with a multitude of paradigms, and the effect of target velocity represents 'one of the most robust influences' <sup>1, p. 828</sup>. For example, Hubbard and Bharucha <sup>10</sup> showed nearly linear increases in visual RM with increases in horizontal and vertical target velocities. This relationship between RM size and target velocity, however, has not yet been clearly demonstrated in audition. Potentially salient differences between paradigms <sup>see 7</sup>, as well as the large variation in the documented size of the auditory RM effect, complicates any comparisons between studies to determine the effect of velocity. Results by Perrott and Musicant <sup>3</sup> do not indicate an effect of target velocity on auditory RM, but the large range of RM reported (-11° to 25°) might mask a potential relationship. Getzmann et al. <sup>6</sup> found a smaller RM for the faster target velocity for targets moving towards the midline, while targets moving towards the periphery resulted in the opposite effect. Such divergent results make it difficult to describe a model underlying auditory RM.

# 9.3. Methods

## 9.3.1. PARTICIPANTS

11 participants (3 female) took part in the experiment, 6 were naïve with respect to the goal of the study. The participants' ages ranged from 20 to 55 years (median 25). Prior to the experiment, participants were informed of the experimental procedures and signed consent forms in accordance with ethics requirements approved by the University of Sydney Ethics Committee.

## 9.3.2. Setup

The experiment was conducted in a 15 m<sup>3</sup> sound-attenuated, darkened room with an ambient noise level of less than 40 dB SPL. Participants sat facing a semicircular wooden frame (radius of 1 m) with their head positioned at the center of the semicircle, and stabilized by a chin rest. A numerical scale (see Figure 9.1) with a resolution of 1° was attached to the wooden frame and encompassed -70° to +70° azimuth. The scale was positioned at the eye level of the participants and illuminated from behind by an LED strip. Grey fixation crosses (3° W x 3° H) were printed on the scale at -25°, 0° and +25°. Below the scale, all tick-marks corresponding to even integers were labelled from 0 to 140.



**Figure 9.1:** (a) The numerical scale. For purposes of illustration only a portion is shown. The grey cross represents the fixation point at -25°. The bars on the scale alternated between green, red and black for greater distinguishability. For details, see text. (b) Verbal instruction for fixation point and corresponding stimulus trajectories for moving targets. The grey area represents the randomized jitter of the endpoint in 1° steps.

At the beginning of each session, lasers were used to position the participant's head in the center of the semicircle, with their nose at 0° azimuth. Headphones (Beyerdynamic DT990) presented the stimuli produced by the digital to analog interface (RME Fireface 400). All stimuli were presented at a comfortable suprathreshold listening level (~60 dB SPL). A head-tracker (InterSense InertiaCube 4) on top of the headphones served to monitor the participant's head position during the experiment. If the head position

deviated by more than  $\pm 1^{\circ}$  in yaw, pitch or roll, the participants were guided by a LED feedback device to return to the correct head position before they could start a trial.

## 9.3.3. Stimuli

All stimuli were generated using VAS. This technique generates realistic, externalized moving sounds by using individualized Head Related Transfer Functions (HRTFs), which contain the participant's binaural cues (interaural time, phase, and level differences), as well as monaural spectral cues, resulting from spectral filtering by the pinna for review, see 11.

Prior to the experiment, HRTFs of 1° resolution were recorded in an anechoic chamber at a distance of 1 m from the participant as per the method described by Carlile and Blackman <sup>12</sup>. To generate moving VAS stimuli, broadband noise (300 Hz – 16 kHz, 5 ms cosine ramps) was convolved with the transfer functions for successive horizontal positions <sup>e.g., see 13</sup>. Velocity was determined by the duration the sound played at each position in space along the trajectory. Moving targets started either at -90° or at +90° azimuth and moved towards the target eye fixation cross at 25, 50 or 100°/s. The target stopped at the fixation point with a randomized endpoint (jitter) of  $\pm 2^{\circ}$  in  $1^{\circ}$ steps, which resulted in five possible endpoints per fixation point. Total target duration ranged between 0.63 and 4.68 s. To be able to subtract other biases in localization, it was necessary to measure the participants' localization bias for stationary sounds. Stationary targets had a duration of 0.2 s and were presented at the fixation point with a jitter of  $\pm 8^{\circ}$  in 4° steps, which resulted in five possible positions per fixation point. The jitter was larger than in the trials with moving stimuli to encompass the range of endpoint values expected to be reported for the moving target, as well as to avoid providing participants information about the jittered endpoint locations for the moving sounds.

# 9.3.4. Procedure

Initially, all participants conducted a listening task that allowed them to practice attentionally tracking the auditory target whilst maintaining eye position. Participants then completed the experiment, which was comprised of 1 training session and 5 test sessions. Each session presented 46 moving trials: 10 warm-up trials and then 36 test trials in a random order comprised of 2 repeats of each unique combination of motion direction, fixation cross, and velocity (2x3x3) for a total of 10 repeats per combination. 40 stationary targets were presented after 36 test trials. To avoid motion aftereffects, stationary and moving trials were not mixed.
Participants pressed a button to start a trial and then received a verbal instruction via headphones to fixate on one of the three grey crosses at 0° and  $\pm 25^{\circ}$ . The sound stimulus was presented 2 s afterwards. In trials with a moving target, participants were instructed to attend to the auditory motion trajectory. Participants verbally reported the location of the moving sound's endpoint by referring to the numerical scale. In trials with a stationary target, participants verbally reported the point on the numerical scale where the target was presented. No feedback was given during the entire experiment. Each session lasted about 10 minutes and the recorded verbal responses were then transcribed and matched with the stimulus for analysis. For each session, we first calculated the mean stationary bias for each fixation point and then corrected the responses for the moving stimuli correspondingly <sup>see 6</sup>. Localization errors in the direction of motion are represented by positive values.

## 9.4. Results

All participants reported well externalized auditory stimuli and no difficulty in attentionally tracking the movement of the target. In a total of three trials across subjects, the verbal responses were inaudible and were excluded from analysis. One participant's results were bimodally distributed indicating a change in response strategy during the experiment which was confirmed on interview. Those data were not included in the analysis.

Using a Generalized Linear Mixed Model (GLMM), we analyzed the factors that influenced the localization of moving targets. The difference between the actual and perceived endpoint of the moving target was the dependent variable. The participants were treated as a random effect, fixed effects represented the target velocity (25°/s, 50°/s, 100°/s), the target direction (left, right), the fixation point (-25°, 0°, +25°), the naivety of the participants (naïve, non-naïve), and all two-way interactions between fixed effects. The size of the RM displacement was only affected by target velocity (p<0.001, GLMM ANOVA), as shown in Figure 9.2(a). Post-hoc pairwise comparisons revealed a significantly larger displacement for 100°/s that reached a mean of 2.27° compared to 25°/s that reached a mean of 0.88° (p<0.001, t-test, Bonferroni-corrected). The lack of an interaction between target direction and fixation point indicates no effect of trajectory length or target duration on RM displacement.



**Figure 9.2:** (a) Displacement in the perception of the point where the target stopped moving (means  $\pm$  SE) in relation to target velocity, illustrated with a linear fit (R<sup>2</sup> > 0.99). Asterisks indicate significant differences in post-hoc pairwise comparisons. (b) Localization error (means  $\pm$  SE) in relation to the difference between target location (stationary sounds) or target endpoint (moving sounds) and the fixation cross. Positive localization errors represent mislocalization to the right of target locations or endpoints, negative localization errors represent mislocalization to the left of target locations or endpoints. To allow for a comparison between target motion directions, localization error for moving targets is defined as corresponding to a rightwards direction of motion. All linear fits reach R<sup>2</sup>  $\ge$  0.97.

Auditory localization was found to be shifted towards the fixation point for both moving as well as stationary targets (Figure 9.2(b)). RM resulted in larger localization errors for the moving targets compared to the localization error for stationary targets, with larger localization errors for faster velocities (see also Fig. 2(a)). The error in localization showed low variance for stationary targets (mean SE = 0.58°) as well as for moving targets if the eye fixation point was taken into account (mean SE: 25°/s, 0.33°; 50°/s, 0.49°; 100°/s, 0.67°), indicating that the perception was highly reproducible between trials and sessions. For stationary targets presented at the fixation point, the mean localization error was 0.19° ( $\pm$  0.41° SE), and the mean standard deviation across participants was 1.64° ( $\pm$  0.34° SE).

### 9.5. DISCUSSION

The effectiveness of the VAS method is demonstrated by a close relationship of the localization errors for stationary targets presented at the fixation points to previously measured free-field localization errors of the auditory system in the frontal region <sup>e.g.,</sup> <sup>14</sup>. Also, the localization errors for stationary targets presented beyond the fixation points showed a low variance. These results confirm the consistent set of veridical target localization cues through VAS. For moving targets, localization was displaced in

the direction of target motion for all three velocities tested, which is strong evidence for a RM effect.

Our results provide strong evidence that both stationary and moving targets were mislocalized towards the grey crosses that served as fixation points (Figure 9.2(b)). The gradients of the slopes for the linear fits are very similar for stationary and moving targets. Also, the distance between the fits for the moving targets resembles the effect of target velocity on the size of RM (see Figure 9.2 (a)). Therefore, for moving targets, the effect of target offset position in relation to fixation point appears to be additive with the RM effect. When this effect of target offset position is accounted for (Figure 9.2 (b)), the variance in localization for the three target velocities shown in Figure 9.2 (a) is considerably reduced. The most likely explanation is that localization was biased towards eye position – although we did not measure eye position, subjects were instructed to hold fixation throughout the trial. Several auditory studies have demonstrated a localization bias towards eye position for stationary targets <sup>e.g., 15</sup>. Except for Mateeff and Hohnsbein <sup>5</sup>, previous studies on auditory RM did not provide participants with fixation targets so the effects of eye position remained uncontrolled. Measuring eye position in future studies on auditory RM would be useful in clarifying this effect.

Our results show a linear increase in auditory RM with target velocity, replicating results from multiple studies on visual RM<sup>1</sup>. The effect of target velocity on visual RM and the range of RM size are similar to our auditory results. Most of these experiments used rotational stimuli rather than translational stimuli, which, to some extent, complicates comparisons with this study. One visual RM study <sup>10</sup> used methodologies comparable to the present study and found visual RM to increase from approximately 0.8° to 2.2° for target velocities increasing from 5.8 and 34.8°/s. In comparison to previous auditory studies on the effect of target velocity on RM, the range of RM size in our study is lower and previous results would not be predicted by the trend shown in Figure 9.2 (a). Unlike all recent studies, which employed action paradigms, we used a perceptual response measurement paradigm to avoid motor response biases. The lower range of RM size in our study is in line with the finding that action paradigms result in larger visual RM size than perceptual paradigms <sup>1</sup>.

Results from stimuli moving towards the midline in the study by Schmiedchen et al.<sup>9</sup> confirm the effect of target velocity found in this study. However, our results do not support the finding that stimuli moving towards the periphery resulted in an opposite effect of target velocity on RM size. The positive relationship between target velocity and RM size found in this study also contradicts the findings by Getzmann et al.<sup>6</sup>, who showed that a slow 8°/s continuous target resulted in larger RM than a faster 16°/s continuous target. The authors hypothesized that the faster moving target may have been insufficient to engage the mechanism underlying RM because the shorter

duration provided less spatial information. A subsequent study by Getzmann and Lewald <sup>8</sup> found that a 16°/s target with identical spectrum but much longer duration resulted in a nearly identically small RM size. This would indicate that target duration per se is not underlying the effect of target velocity on RM size in the study by Getzmann et al.<sup>6</sup>. Indeed, our study did not show an effect of target duration. However, spatial information may play a role in the mechanism underlying RM, which is limited for example by the spatial acuity of the auditory system in the region of target endpoints, or by the target spectrum. Compared to the study by Schmiedchen et al.<sup>9</sup>, localization acuity was higher in regions where targets moving towards the periphery ended. Also, the current study is the first to provide the full range of localization cues by using broadband noise stimuli. Besides the differences in response measurement paradigm described above, these factors influencing spatial information may be underlying the difference in findings compared to the studies by Getzmann et al. <sup>6</sup> and Schmiedchen et al. <sup>9</sup>. The similarities between RM in the present study and visual RM suggests that our stimuli were adequate in engaging the RM mechanism at all velocities examined. Future studies are needed to clarify the effect of spatial information on auditory RM.

This study indicates that the auditory system may possess a predictive mechanism for auditory motion. In addition, the similarity of our results with visual RM suggests that a similar or common mechanism, likely to be high-level <sup>e.g., 2,8</sup>, could underlie both effects. If this were the case, then much could be learnt about auditory motion processing from the significant body of knowledge regarding visual RM. Better characterization of auditory RM and its role in motion processing awaits further research.

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# Erklärung

Darlegung der Anteile aller Autoren an den wissenschaftlichen Einzelarbeiten der kumulativen Dissertation (gemäß §9 der Promotionsordnung)

#### **Eigener Beitrag**

Bei allen in dieser Dissertation eingebundenen Studien war ich maßgeblich an der Ausarbeitung der experimentellen Fragestellungen und der Anpassung der experimentellen Paradigmen beteiligt und war für Aufnahme und Auswertung der experimentellen Daten verantwortlich. Die Manuskripte wurden von mir als Erstautor verfasst.

#### Beiträge der anderen Autoren

#### Experiment I

Georg M. Klump: Mitarbeit bei Konzeption und Ausrichtung der Studie, Mitarbeit beim Manuskript

#### Experiment II

Katharina M. Borzeszkowski: Mitarbeit bei Auswertung der Studie Georg M. Klump: Mitarbeit bei Konzeption und Ausrichtung der Studie, Mitarbeit beim Manuskript

#### Experiment III

Katharina M. Borzeszkowski: Mitarbeit bei Durchführung und Auswertung der Studie Georg Klump: Mitarbeit bei Konzeption und Ausrichtung der Studie, Mitarbeit beim Manuskript

#### Experiment IV

Shannon M. Locke: Mitarbeit bei Konzeption und Auswertung der Studie, Mitarbeit beim Manuskript Johahn Leung: Mitarbeit bei Konzeption der Studie, Mitarbeit beim Manuskript Simon Carlile: Mitarbeit bei Konzeption und Ausrichtung der Studie, Mitarbeit beim Manuskript

# Erklärung zur selbstständigen Verfassung der Arbeit und der verwendeten Hilfsmittel (gemäß §10 Abs. 2b der Promotionsordnung)

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbstständig verfasst und nur die angegebenen Hilfsmittel verwendet habe. Zu den aufgeführten Manuskripten trug ich, wie oben aufgeführt, den Hauptteil bei.

# Erklärung zur Veröffentlichung von Teilen der Dissertation (gemäß §10 Abs. 2b der Promotionsordnung)

Hiermit erkläre ich, dass die vorliegende Dissertation in Teilen bereits veröffentlicht wurde. Eine Publikationsliste ist Bestandteil des angehängten Lebenslaufs.

Arne Feinkohl

# DANKSAGUNG

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