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Contextual plasticity in spatial hearing

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Beáta TOMORIOVÁ

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CONTEXTUAL PLASTICITY IN SPATIAL HEARING

DISSERTATION

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Department:	Department of Cybernetics and Artificial Intelligence (KKUI)
Supervisor:	Doc. Ing. Norbert Kopčo, Phd.
Consultant:	Doc. Ing. Norbert Kopčo, Phd.

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Abstract in English

The thesis examines dynamic processes in auditory spatial perception by human listeners. In order to elucidate how temporal and spatial relationships between stimuli can influence the human ability to localize sound sources, it focuses on a new phenomenon referred to as “contextual plasticity”. This phenomenon shows that performance in a simple task of localizing a single target can depend on the context in which the task is performed. The context is represented by an interleaved more complex localization task, in which the target is preceded by another sound. We conducted two behavioral experiments examining various spatial aspects of contextual plasticity, with the aims of understanding why this effect occurs and what its underlying neural representation is. We found that the context, in addition to inducing biases in localization, provides a more stable and more correlated mapping between the locations of responses and sound sources. This suggests that listeners use spatial information provided by the context in order to improve their performance in a simple localization task. Contextual plasticity was also found to depend on the spatial configuration of the stimuli used in the experiment and in the contextual task. Based on the results it can be inferred that contextual plasticity is induced at later stages of auditory processing pathway at which spatial representation is Cartesian-like, i.e., beyond the stage at which binaural cues are processed and which is based on polar representation. A computational model was developed to describe observed plastic changes. The model assumes that the contextual stimuli induce local biases in the neural representation of auditory space. Several variants of the model were tested, differing in the assumptions about the spatial characteristics of the neural representation and interactions between its units. The model successfully described many characteristics of the behavioral data. These results are important for our understanding of the dynamic processes in auditory spatial perception, which can be useful for various technical and medical applications such as virtual reality, human-computer interaction and auditory prosthetics.

Abstract in Slovak

Táto práca skúma dynamické procesy v ľudskom priestorovom sluchovom vnímaní. S cieľom objasniť, ako môžu časové a priestorové vzťahy medzi stimulmi ovplyvniť schopnosť lokalizácie, sa zameriava na nový jav nazvaný „kontextuálna plasticita". Tento jav ukazuje, že schopnosť vykonávať jednoduchú úlohu pozostávajúcu z lokalizácie jedného cieľového zvuku môže závisieť na kontexte, v ktorom je táto úloha vykonávaná. Kontext je reprezentovaný komplexnejšou lokalizačnou úlohou, v ktorej cieľovému zvuku predchádza iný zvuk a ktorá je prekladaná pomedzi merania s jednoduchou lokalizačnou úlohou. Vykonali sme dva behaviorálne experimenty skúmajúce rôzne priestorové aspekty kontextuálnej plasticity, za účelom pochopiť, prečo k tomuto javu dochádza, a aká je jeho neurálna reprezentácia. Zistili sme, že kontext okrem vyvolania posunov v lokalizácii zlepšuje korelácie medzi pozíciami odpovedí a zdrojov zvuku, a zlepšuje tiež stabilitu tohto mapovania. To naznačuje, že poslucháči používajú priestorovú informáciu poskytovanú kontextom na zlepšenie ich výkonu v jednoduchej lokalizačnej úlohe. Ukázalo sa tiež, že kontextuálna plasticita závisí na priestorovej konfigurácii stimulov použitých v experimente a v kontextuálnej úlohe. Z výsledkov je možné usúdiť, že kontextuálna plasticita je vyvolaná v neskorších štádiách dráhy spracovania sluchového vnemu, v ktorých je priestorová reprezentácia podobná karteziánskej, t.j. za štádiom, v ktorom sa spracovávajú binaurálne parametre, a ktoré je založené na polárnej reprezentácii. Na popísanie pozorovaných plastických zmien bol navrhnutý výpočtový model. Model predpokladá, že kontextuálne stimuly vyvolávajú lokálne posuny v neurálnej reprezentácii sluchového priestoru. Testovaných bolo niekoľko variantov modelu, líšiacich sa v predpokladoch o priestorovej charakteristike neurálnej reprezentácie a interakciách medzi jej jednotkami. Model úspešne popísal viacero charakteristík behaviorálnych dát. Tieto výsledky sú dôležité pre naše pochopenie dynamických procesov v priestorovom sluchovom vnímaní, ktoré môže byť užitočné pre rôzne technické a medicínske aplikácie, ako napr. pre virtuálnu realitu, interakciu človek - počítač a sluchovú protetiku.

Declaration

I hereby declare that this thesis is my own work and effort. Where others sources of information have been used, they have been acknowledged.

Košice, 25. april 2013

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Signature

Acknowledgement

I would like to thank my supervisor Norbert Kopčo for his guidance, patience and encouragement throughout this work. I would like to thank also my friends and family for help and support.

Preface

During my undergraduate studies I became interested in a field of cognitive science because of its interdisciplinary nature interconnecting computer science, psychology, neuroscience and other fields I find interesting. The choice of the topic of my dissertation was motivated by my participation on the research at the Laboratory of Perception and Cognition at Technical University of Košice, which primarily focuses on studying how people perceive auditory space and what brain mechanisms underlie this process.

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List of Symbols and Abbreviations

ANOVA	**an**alysis **o**f **va**riance
CC	**c**orrelation **c**oefficient (abbreviation defined within the thesis)
HRTF	**h**ead-**r**elated **t**ransfer **f**unction
IC	**i**nferior **c**olliculus; brain structure
ILD	**i**nteraural **l**evel **d**ifference
ITD	**i**nteraural **t**ime **d**ifference
MAA	**m**inimum **a**udible **a**ngle
SC	**s**uperior **c**olliculus; brain structure
SD	**s**tandard **d**eviation (abbreviation defined within this thesis)
SOA	**s**timulus **o**nset **a**synchrony

List of Terms

lateral	situated at, or on the side
binaural	relating to two ears
monaural	relating to one ear
interaural axis	axis connecting the ears
crossmodal	relating to different sense modalities

Introduction

Brain processing is dynamic, adapting at many time scales in order to correctly accommodate to various changes, both internal (e.g., physical changes during growing up, or sensory loss/impairment) and external (changes in the environment). There are many mechanisms that enable this adaptation and their understanding is important for many purposes. For example, in medicine, for treatments of brain damage (indicating how brain can be reorganized to substitute for lost abilities, how can the reorganization be affected by training, etc.), or in sensory prosthetics (indicating sensitive periods during which the brain is more able to adapt). Understanding brain dynamics on a shorter time scales can be useful also for various technical applications, for example robotics (indicating how should robot adjust to changing environments), or virtual reality. In this thesis, we will focus on the plasticity in the auditory domain.

Our inner representation of auditory space is not fixed but undergoes changes. These changes can be related to adjustment of localization due to developmental changes (i.e., inner representation adjusts according to anatomical changes of the head whose shape is important factor in process of sound localization) [46][2], or adaptation to current environment (for example, auditory system suppresses spatial information of sound which is considered to be an echo) [71]. However, several changes in sound localization were observed which result not in improvement, but in erroneous localization of a sound, and even though their purpose might not be understood, they provide a better picture of the nature of sound localization processing. Among the examples are studies, in which bias in localization was induced by prolonged exposure to adapting sound [24][25][26][78], by misleading feedback [22][23], manipulations with visual field [70][29], and pairing the sounds with visual stimuli [9][10].

It is not yet understood which brain mechanisms are responsible for plasticity in sound localization and one of the reasons is that there is a great variability among the plasticity studies, each of which possibly describes different phenomenon. For example, developmental plasticity may occur at different spot in sound localization pathway and may be based on different processes than plasticity caused by prolonged adapting sound. Possibly different mechanisms are reflected also in different time scales in which plasticity develops and disappears – both longer (few weeks or days) or shorter time scales (few minutes) were observed.

One group of plasticity studies is focused on how localization of a sound is influenced by preceding exposure to another sound, so-called “adaptor” [24][25][26][78]. It was shown that responses on target sounds are shifted away from adaptor location.

Even though not considered as studies of plasticity due to very short time scales, studies related to famous precedence effect also show that perception of target is not static but undergoes changes due to preceding sound (distractor)) [71]. In this case, with shorter time delays between distractor and target sounds, response on target is attracted towards the distractor location.

Current thesis was motivated by one of the studies examining effect of preceding distractor, Kopčo et al. [64]. Distractor could come from frontal or lateral location and its location was fixed within an experimental run. As authors expected, distractor caused biases in localization of subsequent target. But unexpectedly, they also found that responses on interleaved control trails, in which only the target was presented, and which were therefore considered to be a reference not influenced by distractor, differed when the control trails were presented in context of trials with frontal-distractor versus lateral-distractor. Since localization of targets in control trials seems to be influenced by context of interleaved distractor trials, authors referred to this effect as “contextual plasticity”.

In this thesis, we focus on spatial aspects of the contextual effect. Two experiments were performed, in which we varied: 1) location of the distractor relative to the listener, 2) spatial configuration of the contextual stimuli, and 3), tested region of space relative to the listener. Through these spatial aspects we examined the nature of spatial representation on which the contextual plasticity operates and possible causes of the contextual effect.

Finally, we designed a model which quantitatively describes contextual biases observed in the two experiments, considering a possible mechanism of how the effect is induced in the underlying spatial map.

1 Aims of the study

Aims of study the can be summarized as follows:

- **Design of behavioral experiments which will examine spatial aspects of the "contextual plasticity" phenomenon, observed in [64].**
  - The experiment will be designed which allows to test the effects of: 1) location of the distractor relative to the listener, 2) spatial configuration of the contextual stimuli, and 3), tested region of space relative to the listener.
- **Evaluation of the contextual effect and of its dependence on specific spatial manipulation of the contextual stimuli.**
  - Evaluation will be based on computing biases of responses in conditions "with context" relative to responses in control condition in which no context was provided. Experimental conditions with different spatial manipulations will be statistically compared.
- **Design of a quantitative model of contextual bias based on observed results.**
  - The observed contextual bias will be quantitatively described by a model, which would also consider possible mechanism of how the effect is induced in the underlying spatial map.
- **Evaluation of the model on the observed data.**
  - Mean standard error will be computed between the best-fit provided by the model and the data.
- **Discussion of the results with other related studies of plasticity in sound localization**

2 Theoretical background

2.1 Sound localization

This chapter describes how human listeners localize sound sources. In auditory perception, the information about the location of a source is not provided as directly as in visual perception, in which the external world is topographically projected onto the retina and this topography is maintained in further processing. In auditory perception, sound location has to be computed indirectly, e.g. by comparisons of inputs between the two ears. In this chapter, we will introduce the cues that listeners extract from incoming sound and which serve as a basis for estimation of the position of the sound source. We will also mention neurophysiology of sound localization - which brain structures are involved in this process and what function these structures have.

Sound source can be localized in three dimensions: horizontal, vertical, and distance. This thesis is focused on horizontal localization, thus the bigger part of the theoretical background will be dedicated to this topic while localization in other two dimensions will be mentioned just marginally.

2.1.1 Localization in horizontal plane: binaural cues ITD and ILD

Localization of a sound source in horizontal plane is based on the fact that sound presented off the midline will reach each of our ears in slightly different form. One ear is closer to the sound source than another and the sound will arrive in the closer ear a little bit sooner and more intense than in the more distant ear. The difference in time is given by different distances the sound has to travel to each ear and the difference in intensity is produced by the head which acts as a barrier and attenuates (or “shadows”) the sound.

Auditory system captures these differences in time of arrival and intensity (ITD = interaural time difference and ILD - interaural level difference) and on their basis estimates the position of the sound source [42]. These cues are referred to as binaural cues, because they are based on comparison of signal from both ears. Specific values of ITD and ILD are associated with specific positions in horizontal plane. For example for ITD=0 and ILD=0 (sound arrived in both ears at the same time and with the same intensity), listener perceives the sound as coming directly from the front or from the back. With increasing differences the perceived position shifts to the side, while the maximum (azimuth +/- 90°) is reached for ITD equal to approximately 0.6 ms [14]. Maximum value for ILD depends on frequency - can be very small at low frequencies but can be above 15 dB for frequencies higher than 2000 kHz [44]. Mapping between specific ITD, ILD and position in space is specific for each listener because these cues depend on shape of the head.

It is presumed that we do not use ITD and ILD for sound localization in an equal manner, but rather choose ITD for sounds at low frequencies and ILD for high-frequency sounds [11][63]. Because of this, broadband noise is often used in experiments - since it consists of low and high frequencies, listener can use both ITD and ILD cues for localization and the sound becomes easier to localize [67].

2.1.2 Cone of confusion

Binaural cues by themselves aren't able to specify the location of the sound clearly - there still exists an ambiguity given by way how localization cues are achieved. The reason is that positions symmetric around the axis connecting both ears (so-called interaural axis) have the same or very similar values of ITD and ILD (for example, sound coming from azimuth 80° will have the same values of binaural cues as the sound coming from 100°) and auditory must decide which of the concurrent positions for specific ITD, ILD is actually the correct one.

If we generalize this situation into 3-dimensional space, ambiguous positions for specific ITD or ILD form a cone, so-called "cone of confusion" centered on the interaural axis [42]. Also behavioral studies confirm that cone of confusion affects localization performance, for example in horizontal sound localization it results into front-back confusions [11].

2.1.3 Localization in vertical plane

While primary cues for horizontal localization were based on cues comparing signals from both ears (i.e., on binaural cues), vertical localization is based on signal from one ear only (monaural cue), specifically on the shape of the spectrum of arriving sound [42]. Before the sound reaches ear canal, it is transformed by reflections from shoulders, head, ear folds, etc., and depending on the position from which it arrives, certain frequencies are suppressed or enhanced. Particular pattern of spectral alternation is therefore associated with particular vertical position in space.

Spectral cues can also help solve the front-back confusions [11]. For example, when ITD, ILD=0 the sound coming from behind is due to the shape of the ear shadowed more than the sound coming from the front and depending on it the auditory system can choose among the two ambiguous positions.

2.1.4 Distance perception

Several cues are considered to play role in judging the distance of a sound (review in [66]). One of the primary cues is the sound level. Sounds with higher sound level appear closer than sounds with lower sound level. Except for this cue we also use sound reflections – auditory system computes energy of direct sound and energy of reverberation. The greater is the direct-to-reverberant energy ratio, the closer the sound appears. Spectral shape can also provide some information. Since high frequencies are more attenuated as the sound travels to the listener than low frequencies, the greater the content of high frequencies in the signal, the closer sound appears.

These cues help us to estimate whether a sound is relatively closer or farther than some reference sound, i.e. they seem to be not sufficient for absolute localization. However, when sounds become familiar in the sense that we know their typical spectrum or sound level, absolute localization is possible.

2.1.5 Horizontal localization in complex environments

Localization of a single sound source in an anechoic space is different from localization in reverberant environment, because the direct sound acoustically interacts with its echoes, which come from various directions (and therefore have different values of localization cues) as the sound reflects from the walls, floor, other objects, etc., and from this mixture listener must identify where the original sound source is.

2.1.5.1 Precedence effect

Even though the task of localizing a sound source in reverberant environment is difficult and mixture of different values of localization cues produced by echoes should result in listener’s confusion, it is the task which we solve daily and automatically. It is believed that the phenomenon called **"**precedence effect**"** (review for example in Litovsky et al. [71]), observed in many psychophysical studies is responsible for solving this task.

The precedence effect occurs when two sounds from different locations are presented successively with specific delay between them (similar to direct sound and its echo), and it stands for the situation, that spatial information from the latter sound is suppressed and the two sounds are fused into a perception of a single auditory object, originating from the leading sound's location.

Depending on the delay between the two presented sounds, different perceptual effects can be observed: If a sound is presented simultaneously from two locations, the single fused image will be perceived from the location in the middle between the two actual locations. When we increase the delay between sounds, the image remains fused and it shifts towards position of a leading sound, reaching it at delay of approximately 1ms (the precedence effect). When the delay crosses 5 ms (or more, even 50 ms, depending on type of the stimulus), fusion breaks and we start to perceive two separate sounds. This upper boundary of the delay upon which the precedence effect operates is also often reffered to as "echo threshold".

2.1.6 Simulations of auditory space

Sound localization studies often use virtual auditory environment (i.e., simulations of auditory space through earphones) instead of real environment. Advantage of virtual auditory environment is that ITD and ILD of a presented sound can be manipulated independently of each other (ITD by presenting sound with specific delay between left and right ear, and ILD by presenting it with specific difference in intensity), while in real environment they are tied together. This allows studying the effect of each of them separately. In general, virtual environment gives the experimenter better control over the presented stimuli and it makes stimulation more replicable from subject to subject and trial to trial.

However, manipulating only ITDs and ILDs of a presented sound is not sufficient to create a percept that a sound is coming from external space. Instead, sound is perceived as originating within head [11]. In order to externalize the sound, its spectrum must be changed similarly as spectrum of an external sound is changed by interactions with the body of the listener (with arms, head, outer ears, etc.). The transformation which sound undergoes as it travels from its source to the eardrum can be described by so-called head related transfer function (HRTF). Each point in space is associated with a pair of HRTFs, one for the left and other for the right ear. Mathematically, HRTFs (H_l and H_r, for the left and right ear, respectively) for a sound source located at azimuth φ and elevation θ in a spherical coordinate system, can be defined as a frequency-dependent ratio of the sound pressure level at the eardrum $\Phi_{l,r}$ to the free-field SPL at location where center of the listener's head would be [82] (see equation (1)). If HRTFs for a specific point in space are known, we can create a perception that a sound is originating from this point by filtering the sound with appropriate HRTFs.

$$H_l(\omega,\varphi,\theta) = \frac{\Phi_l(\omega,\varphi,\theta)}{\Phi_f(\omega)}, \qquad H_r(\omega,\varphi,\theta) = \frac{\Phi_r(\omega,\varphi,\theta)}{\Phi_f(\omega)}. \qquad (1)$$

Since HRTFs depend on shape of ears, head, etc., they are individual for each listener. Hence, if HRTFs measured on one person are applied on somebody else, she/he may perceive it from different location. Therefore individualized HRTFs are often used in psychoacoustic experiments.

To incorporate also the transformation of the sound due to interaction with room (caused by reflections from walls, floor, etc.), so-called binaural room impulse response functions (BRIR) are used [83]. Similarly to HRTFs, BRIRs are expressed in pairs, one for each ear. By convolving any non-reverberant sound with BRIR functions, one can induce a perception that the sound was presented from a specific location in a specific room.

2.1.7 Accuracy of sound localization

Accuracy of sound localization can be assessed by several different types of measurements. Accuracy in localization task using pointing method of responding (subjects pointed to a perceived sound location) is best for sounds coming from the front - approximately 2°, while for sources more towards the side the accuracy drops to approximately 6-10° [38]. If subject's task is not to localize sound but to indicate whether two sound differ in their spatial locations (discrimination task), measure called minimum audible angle (MAA) is often used. MAA is the smallest angle between two sources which can be reliably discriminated. In accordance with pointing accuracy, it was shown that spatial resolution is better at front (MAA = approx. 1 degree) and decrease at the sides (MAA = 6 degrees) [62].

2.1.8 Neurophysiology of sound localization

Neural processing of sound begins in a snail-shell-shaped structure called cochlea in the inner ear. Sound waves transformed into mechanical movement of middle-ear bones induce pressure waves in fluid inside cochlea, which cause vibration on part of the cochlea called basilar membrane. Depending on frequency of the signal, maximal vibrations are generated on different locations at the basilar membrane. Top of the basilar membrane is cover with hair cells, which are connected also to fibers of auditory nerve. When basilar membrane vibrates, hair cells bend what generates impulse in the fibers [11]. Since specific location on a membrane vibrates maximally only for specific frequency, different auditory nerve fibers are tuned to different frequencies and this tonotopic organization originating in cochlea is maintained throughout many other stages of spatial auditory processing.

Auditory nerve sends signal into the brain for further processing. Further processing includes many stages, but here we will discuss (in a simplified manner) only stages related to horizontal sound localization. It is important to note that most knowledge about neurophysiology of sound localization is based on animal studies which might reveal processes, which are in some aspects similar to, but not necessarily correspond to, human sound localization.

Areas related to horizontal sound localization could be traced in sound processing pathway by finding neurons which are sensitive to inputs from both ears, since it points to the ability to process binaural cues. First brain structure in sound processing pathway presumed to be related to the process of localization is superior olivary complex (SOC) in brainstem. SOC consists of medial superior olive (MSO) and lateral superior olive (LSO) [4]. Neurons in MSO receive excitatory inputs from both ears and each neuron fires with the greatest rate for specific interaural delay of the inputs, i.e., MSO is related to ITD processing [50]. In most cases, neurons in LSO receive excitatory input from ipsilateral ear and inhibitory input from contralateral ear and firing rate changes as a function of interaural level differences (with lowest when it receives equal inputs from both ears), i.e., LSO is related to ILD processing [51]).

Outputs from these two separate branches each computing sound location according to specific localization cue should meet and combine somewhere further in the processing pathway to provide one percept of sound location. A structure, which is considered to be a place of integration, is inferior colliculus (IC) residing in midbrain, in which neurons sensitive to multiple localization cues have been found (in cats [52]).

Most connections from IC are heading towards front brain and superior colliculus (SC) in the midbrain. In deep layers of SC, a topographic representation of auditory space (a point-to-point map) was found in mammals (guinea pigs [68], cats [55], ferrets [88]) and owls (in avian analog of SC called optic tectum (OT), even though the first signs of a topographic spatial map were observed in earlier stage of processing, specifically in external nucleus of IC (ICX), which projects to OT [59]). Except auditory input, deep layers of SC receive also visual and somatosensory inputs, which also form maps of space. These maps are aligned to form a common representation of space [86]. The main function of SC is considered to be control of orienting movements towards an object of interest (for example, turning head or eye gaze towards a sound).

Mentioned brain structures show that major part of spatial auditory perception is related to subcortical regions and existence of spatial map in SC suggests that localization process is almost complete at the level of midbrain [1]. However, higher structures contribute to localization too, specifically auditory cortex. It was confirmed by studies which show that lesions in auditory cortex lead to deficits in sound localization. In animal studies, deficits in contralateral hemispace were observed but in humans deficits are not always restricted to contralateral hemispace [69]. However, most neurons in auditory cortex have very large receptive fields (i.e., one neuron codes large area of space, even whole hemifield [61][1]) what is in contrast with localization acuity measured in behavioral experiments. Moreover, no topographic spatial map has been found in the auditory cortex. In other words, units are not ordered along the cortex according to their spatial tuning, but are dispersed.

In summary, auditory system does not directly code location of space in peripheral stages of processing as opposed to, for example, visual system, where topographic representation is maintained from retina. Instead, tonotopic representation is maintained in auditory system and location of sound has to be “computed”. In mammals, first topographic map of auditory space which codes sound location by locus of activation on the map appears in SC, however, in the latter stages of processing (cortex) this “place code" is no longer preserved and it seems that the location has to be computed differently. So-called "rate code" model, based on comparisons of firing rates of left-tuned and right-tuned neurons is often discussed to underlie localization at this stage of processing. These two types of models (place code and rate code) will be described with more detail in chapter 2.3 Models of sound localization and plasticity.

2.2 Plasticity of sound localization

In previous chapter we mentioned cues which listener extracts from the sound and on their basis computes the position of a sound source. In this chapter, we will discuss studies which show that this mapping is not fixed and that sound coming from specific location can be associated with new different perceived/responded position. We will describe why are these changes in localization necessary, characterize them in terms of how quickly they are induced (after few-days training or within a few minutes), how long they persist (short-term lasting several seconds, or long-term lasting several days or weeks), the way of how they were induced (misleading feedback, a change in localization cues, other auditory stimuli, etc.) and what's their neurophysiological background.

2.2.1 Importance of plasticity

Auditory system should be consistent in localization and should not underlie random changes. But what if, for some reason, the mapping becomes incorrect? Then the plasticity in spatial auditory perception enables listener to adapt to a change and associate specific positions to new correct values of localization cues. One of the reasons why the mapping should be plastic are changes associated with development. As child's head grows the values of binaural cues corresponding to particular position change [46][2]. To maintain correct localization, the mapping should be able to change.

Another example is a change in acoustics of an environment. Everyday we encounter various environments with different acoustics which distract localization cues, since the input to the ears is except for the direct sound also the reverberation (from walls, ceiling, etc.). These reverberant sounds come from various directions and they cause that values of localization cues for specific location vary in time. Auditory system should be able to cope with these variations and recalibrate quickly after entering new room [16] so that localization would be accurate.

Plasticity would be beneficial also in case of a malfunction affecting extraction of localization cues (for example if the intensity of the signal in one ear is reduced due to disease or ear occlusion) [2].

2.2.2 Studies of plasticity

Plasticity is studied on various levels, from low such as molecular, neural, to higher, behavioral level. It can be induced experimentally by several means, for example by manipulation of localization cues elicited by sound, by misleading feedback, by changes in visual field (which can be also considered as a form of misleading feedback), by pairing auditory stimulus with misaligned visual stimulus, or by other auditory stimuli. Several studies falling into these categories will be described in the following sub-chapters.

2.2.2.1 Manipulation of localization cues elicited by sound

One of the ways to induce plasticity in sound localization is to change values of interaural cues which are produced by sound from particular position in space. Trivial example is to occlude one ear - this causes that the intensity of sound in occluded ear will be lower which results in different interaural difference in intensity (ILD) than before ear covering. Experiments on owls using ear occlusion showed that initially, owls mislocalized sounds (away from occluded ear) but auditory system of young owls after several weeks of occlusion adapted to this change and owls learned to localize correctly [53].

Effect of altering localization cues associated with particular location in space was examined also on human subjects. For example, Hofman et al. [35] studied plasticity by covering outer ear with molded mask with artificial folds which were different than folds on subject’s ears. Folds on ears affect spectral characteristics of incoming sound depending on its position in vertical plane and on this basis we are able to localize sound in vertical plane (see chapter 2.1.3 Localization in vertical plane). Mask disrupted previous mapping between spectral characteristics of a sound and its elevation and plasticity was needed to learn new correct mapping. It was shown that after 20-30 days, subjects learn to localize correctly. Moreover, when mask was removed, adaptation was not such slow as before but was immediate, what suggests that after application of a mask previous mapping was not rewritten but both mappings co-existed in auditory system and subjects could switch between them.

2.2.2.2 Rearranging spatial cues by misleading feedback

Another way how to induce plasticity is to provide misleading feedback to subject's localization responses. In this case subjects don't have to adapt to new correct mapping, but instead they are trained to respond according to new abnormal mapping (for example, for sound presented from azimuth 30°, they are given feedback that it originates from 60°). In headphone studies by Shinn-Cunningham et al. [22][23], subjects identified direction of sound stimulus. Sound stimuli were by feedback paired with such locations, which did not correspond to locations normally associated with localization cues of the sound stimuli. Subjects were able to learn new mapping also in this case (even though not completely), which shows that simple feedback (even though misleading) is sufficient to induce short-term changes in sound localization.

Moreover, in separate experiments of this study the rearrangement of spatial cues was achieved instead of an after-trial feedback, by interleaved training runs, during which the auditory stimuli were paired with simultaneous displaced visual stimuli. In other words, instead of a feedback which trained listeners to adapt to new rearranged localization cues in previous case, now adaptation was induced spontaneously without any feedback specifically instructing where the position of the sound source is. How and why adaptation can be induced by providing simultaneous displaced visual stimulus is described in following chapter.

2.2.2.3 Presenting spatially disparate visual stimulus simultaneously with auditory stimulus (or manipulations with visual field)

Plasticity in sound localization can be induced also using visual stimuli. It stems from the fact that our perception of the environment is based on inputs from different sensory systems and in order to create single unified representation of our environment, our brain has to combine the information from different senses. An example of how the brain copes with the fact, when the information from different senses is not correlated, can be observed on crossmodal interactions between audition and vision. It was shown that when spatial information about some object provided by auditory and visual modality is conflicting (i.e., auditory system suggests that object is at location X and visual system suggests that object is at location Y), visual modality "wins" and auditory percept is adjusted according to it [9]. Typical example is so-called **ventriloquism effect** – a puppet in ventriloquist's hand appears to be talking, even though the speech comes from ventriloquist's mouth. This phenomenon has been studied experimentally such that both auditory stimulus and visual stimulus are presented simultaneously (for example, LED light presented simultaneously with noise), while visual stimulus is displaced relative to auditory stimulus and subject's task is to localize the auditory stimulus (and ignore the visual stimulus). Comparing responses with control condition in which only auditory stimulus is presented reveals that subjects' responses on audiovisual trials are shifted by few degrees towards the visual stimulus [9].

The idea that the ventriloquism effect is not only some adopted strategy of responding but that it is accompanied by changes at the perceptual level can be observed on so-called **ventriloquism aftereffect**. In aftereffect studies, subjects typically undergo a period of adaptation in which displaced audiovisual stimuli are presented (as in ventriloquism effect studies). Before and after the adaptation period auditory-only stimuli are presented. It was revealed that changes in sound localization caused by ventriloquism effect persist for some time even after the adaptation period, despite the absence of simultaneous visual stimulus [9][10]. Ventriloquism aftereffect can be therefore considered as another example of plasticity in auditory localization.

Ventriloquism effect and aftereffect are often examined in a basic situation in which only simple auditory and visual stimuli are used to create the conflict between auditory and visual spatial information about the same "object". However, the conflict can be created also by different, more direct, way – by **manipulations with the visual field**.

Knudsen et al. studied plasticity induced in baby owls raised with prisms which shifted their visual field (review of studies in [70]). Studies revealed that sound localization shifted towards the direction of visual displacement and thus provided evidence that owl's auditory spatial map is calibrated according to visual spatial map.

Studies of a calibration of an auditory spatial map by visual spatial map were performed also on human subjects. For example, Zwiers et al. [29] studied effect of compressed spatial vision on sound localization. In this study, subjects were wearing glasses which compressed their spatial visual field by half, for a period of 2-3 days. It was found that auditory localization was compressed according to compression in visual field, but compression was observed only for locations within visual field of the lenses. However, locations outside the visual field of lenses were affected too, even though not by compression but by central shift.

2.2.2.4 Other auditory stimuli

Plasticity in sound localization has been observed also due to presence of other distracting/adapting stimuli, which don’t have to be presented simultaneously with the target to affect its perceived location. One group of studies examines the effect of prolonged exposure to adapting sound (lasting several milliseconds/seconds) on subsequent target localization. Exposure to the adapting sound causes that subsequent target is localized away from adaptor’s location, i.e., adaptor “repulses” the target [24][25][26][78]. This effect is often referred to as “auditory localization aftereffect”. The aftereffect is considered to be the result of “fatiguing” of spatial representations corresponding to adaptor.

The aftereffect has been observed for ILD-only as well as ITD-only stimuli [25][26].

In addition to horizontal sound localization, similar effect was studied also in vertical sound localization by Getzman [27]. A “frame” sound was presented before or simultaneously with target in position below or above the possible target locations. Again, responses on targets shifted away from the frame. That the localization aftereffect can be observed in both horizontal and vertical dimensions was confirmed also by Carlile et al. [24] who showed that responses on targets were radially displaced away from adaptor.

Another aspect of the localization aftereffect is that the adaptor should be similar to target in order to induce an effect. For example, Kashino and Nishida [26] found that the largest adaptation shifts were observed for target and adapter tones of similar frequencies, and with increasing difference in frequency between the tones the shifts decreased [26]. Similarly, Getzmann [27] found that adaptation effect strongly decreased when targets and adapting stimuli were dissimilar (“frames” consisted of square waves and targets of pink noise) as opposed to when they were same (both pink noises or square waves). These results indicate the locus in auditory pathway where the effect occurs, specifically that it is on such level of spatial representation in which different frequency channels are not yet integrated.

Other example of how sound localization is affected by other sound stimuli can be demonstrated on adaptative changes related to the phenomenon called precedence effect (see sub-chapter 2.1.5 Horizontal localization in complex environments) which states that when two sounds are presented sequentially with specific delay between them, we perceive the two sounds as fused and as originating from the location of the first sound. Precedence effect is useful for localization in reverberant environments, where it helps to suppress spatial information from echoes. However, we daily encounter different environments (with different reflections) and therefore the lead-to-lag time interval, on which the precedence effect operates, should be able to adapt to current environment. Consistent with this, Freyman et al [74] showed that precedence effect is able to build up even for such inter-click delay which normally leads to perception of two separate sounds from two different locations. The build-up of the precedence effect (or, shift in the echo threshold to higher inter-click delays) was achieved by presenting a train of identical click-pairs before the target.

2.2.3 Temporal aspects of plasticity

How long does it take to induce plastic changes? And how long do they last? If we take into consideration previously mentioned examples of situations in which the plasticity is important, for some of them slow adaptation would be sufficient (developmental changes, hearing disorders/loss), for other the adaptation should be very fast, within seconds, minutes (changes in acoustics of environment, etc.). Indeed, among the mentioned studies adaptation occurred at different time scales (which might not represent minimum interval for the build-up of plasticity but only some under which plasticity was observed), from several weeks (monaural occlusion in owls [53], outer ears modified with molds, in humans [35]), days (adjustment of auditory space according to compressed visual space [29]), minutes or even seconds (ventriloquism aftereffect [10], adapting to supernormal localization cues [23], build-up of echo suppression [74]). According to this we distinguish between long-term and short-term plasticity and it seems that different mechanisms are responsible for each of them.

2.2.4 Mechanisms of auditory localization plasticity

Auditory localization plasticity observed behaviorally was in many cases found to be associated with structural changes in the brain. For example in owls raised with prisms shifting their visual field, auditory spatial map adjusts to match visual spatial map by realigning auditory receptive fields of neurons in optic tectum with their visual receptive fields. This realignment is accompanied by axonal remodeling of neurons which project from inferior colliculus (ICC) to external nucleus of inferior colliculus (ICX) [84]. Normally, projections between ICC and ICX are topographic, but following experience with prisms, neurons in the ICC which represent such ITDs which were shifted, projected their axons to neurons in new regions of ICX, and hence also affect their tuning. Spatial changes from ICX are transferred to OT.

Similarly, changes in neural tuning were observed when plasticity was induced by occlusion of one ear of owls [85].

Such spatial remodeling requires longer time to build-up, however, changes in spatial representation at much shorter time-scales were also observed. For example, neurons in the auditory map of owls, in a response to moving sound, shift their receptive fields towards the approaching sound [92].

In humans, neurophysiology of brain processes is examined through various brain imaging techniques, for example by measuring electrical activity of the brain using electrodes placed on the scalp, technique referred to as electroencephalography. Measured brain response to a specific stimulus is called event-related potential (ERP). Changes in localization observed behaviorally are associated with modulations of ERPs, suggesting that they are accompanied by changes at neural level. For example, ventriloquism aftereffect is associated with modulation of ERP approx. 100 miliseconds after the presentation of the stimulus [87].

In studies of in which the adaptation is induced by prolonged exposure to adaptor, adaptation is explained by a “fatigue” of neural representations underlying adaptor’s location [24][78][89].

2.3 Models of sound localization and plasticity

There are many models of sound localization. Most of them are focused only on a specific phenomenon or specific stage of localization processing. Some models are aimed to model physiology, neural activity, other are psychophysical or combined. Here we will mention two groups of models which consider different coding of sound location. **Place code models** assume that there is a topographically organized map of many channels each tuned to specific spatial location, and location of a sound is represented by neural activity at restricted area of the map. The **rate code models** (or, often called "two channel models" or "hemifield code models")**,** on the other hand, assume there are two channels each preferentially tuned to specific hemisphere and sound's location is determined by comparison of the activity of these channels.

2.3.1 Place code models

2.3.1.1 Jeffress model

The earliest place code model was proposed by Jeffress in 1948 [57] and became a classical model of binaural interaction and basis for most future models [80]. This model explains how the brain extracts the ITD information from incoming sound. The model consist of an array of special cells, called "coincidence detectors", which get input from both ears and fire only when these inputs arrive to them simultaneously. The signal from each ear travels to the detectors along a series of delay lines of various lengths. According to their length, delay lines "postpone" a signal. Different combinations of relative length of left-ear delay line versus right-ear delay line represent tuning of particular coincidence detector to specific ITD (because if signal which arrived earlier is delayed relative to signal from other ear by time equal to ITD, the signals meet in the coincidence detector at the same time and coincidence detector will fire). Jeffress assumed that coincidence detectors are organized in a "space map", i.e., neighboring detectors code neighboring positions in space. The spatial position of the source is determined in the array of coincidence detectors as the locus of maximal activity.

2.3.1.2 Colburn's quantification of Jeffress model

Jeffress model was only conceptual and did not specify exact mechanism of computation. Later, some models were developed which expressed Jeffress model in quantitative form, for example, model by Colburn (reviewed in [75], [6], [76]). Colburn's model consists of two parts, model of auditory nerve activity and model of central processing. We will focus only on second part of the model which is directly related to localization. Colburn's model involves coincidence detectors, each of which is associated with specific internal time delay τ (corresponding to delay lines in Jeffress model), which shifts one input spike train relative to the other. If spikes occur simultaneously (or almost simultaneously) coincidence detector will fire.

Average number of these "coincidences" for a coincidence detector with specific internal delay τ is an estimate of the cross-correlation function of the neural inputs arriving into the coincidence detector, evaluated at the delay τ. As mentioned in previous chapters, auditory signal is initially processed in separate frequency bands, which is also considered in the model. Cross-correlation function is computed separately in each frequency band and then integrated across the frequency bands into summary cross-correlation function. Perceived position is estimated either according to locus of peaks in final cross-correlation function or locus of centroid along the internal delay axis.

Computation of a coincidence according to cross-correlation function is shown in equation (1). Average number of coincidences observed in time t for all fibers with characteristic frequency f and delay τ, $E[L(t,\tau,f)]$, is

$$E[L(t,\tau,f)] = \int_{-\infty}^{t} r_L(\alpha) r_R(\alpha-\tau) w_c(t-\alpha) p(\tau,f) d\alpha \qquad (1)$$

in, $r_L(t)$ and $r_R(t)$ are inputs to coincidence detectors, $w_c(t)$ is temporal weighting function and $p(\tau,f)$ is relative number of coincidence detectors with internal delay τ and characteristic frequency f, $E[\cdot]$ denotes expectation and $L(t,\tau,f)$ is a binaural decision variable [76].

In Colburn's model, cross-correlation is performed on neural responses generated by auditory stimuli. However, there are other models, in which cross-correlation is computed directly from auditory stimuli (reviewed in [76]).

2.3.2 Rate code models

In another group of models, so-called rate-code models (describe for example in [81][77]), sound location is not coded by locus of activity on a topographic map of neurons, as in the place code-models, in which each neuron had a narrow restricted receptive field. In rate-code models each neuron responds to very large range of sound locations but is preferentially tuned to left or right hemisphere. Specifically, it responds monotically with changing azimuth according to sigmoidal function and sound location therefore cannot be deduced from locus of activity. Instead, sound location is computed by comparisons of activities from left-tuned versus right-tuned neurons.

Rate-code models are often used to model ILD computation but also for modeling of how space is coded in auditory cortex [77].

2.3.3 Models of plasticity in sound localization

Depending on coding strategy (place code versus rate code) considered, different models of plasticity in sound localization exist.

Carlile et al. [24] found that exposure to adaptor caused shifts in responses on subsequent target sounds. To explain the shifts, he proposed a model based on a place code. The model consists of topographically spaced array of units (neurons) each tuned to specific spatial location. Receptive fields of neurons partially overlap each other. The perceived location of a sound is determined by "ensemble output" of subpopulation of units activated by the sound from particular location, with mean activity centered at that location. Carlile et al. suggested that adaptation bias arises from the fact that prolonged exposure to adaptor sound down-regulates subpopulation of units associated with the adaptor's spatial location. Balance of the ensemble output is then disturbed and locus of mean activity for sounds associated with units close to adaptor is shifted away from adaptor. However, Carlile's et al. model is only conceptual.

Similar model of adaptation due to „fatiguing“ adaptor, even though not only conceptual but quantitative, was proposed by Kashino and Nishida [26]. Stimuli in their experiment were lateralized only according to their ITDs. Consistently with other studies with preceding adapting sound, adaptor caused repulsion of subsequent responses away from it.

Different approach to explain shifts caused by adaptation was used for example in in [78] or [89]. They plastic changes in localization caused by exposure to adaptor were observed not only for locations close to adaptor but for locations across entire auditory hemifield, which supported the model of adaptation based on a rate-code. Except for common two-channel model with two groups of neurons broadly tuned to left or right hemifield, Dingle et al. [78] proposed even three-channel model with a third, midline-tuned channel.

2.3.3.1 Evidence for models

Evidence for both models was found at various stages of sound localization processing. Place code was observed in SC of mammals [55],[68] and also in IC [58] and optic tectum (equivalent to SC) of owls [59]. Moreover, it was revealed that the space is not encoded in these maps uniformly, but that frontal locations are encoded by larger number of neurons than lateral locations and that they have also narrower receptive fields [59].

Rate code identified by large receptive fields was observed for example in LSO (structure in which ILD processing takes place) of cats [90], but also on higher, cortical, areas (monkeys: [77]). Even though non-invasive methods used for studying human brain do not allow examining tuning of single neurons separately, magnetoencephalography (MEG) experiments revealed evidence for a rate code (for ITD) also in human auditory cortex [81][89].

Taken together, the coding strategy for sound localization in humans is still not known, especially at lower stages of processing. However, at higher (cortical) stages, a rate code model seems to be appropriate.

3 Experimental part

In this section, we present two experiments which we conducted in order to study plasticity in sound localization. The studies examined “contextual plasticity”, a new phenomenon described in [64] . The experiments focused on examination of the spatial aspects of the contextual effect. Several analyses of the spatial dependencies of the effect are described in this section. They provide possible explanations of why the effect occurs and what its possible underlying neural representation is. Before the description of the two experiments, a short summary of the original “contextual plasticity” study [64] is presented.

3.1 Introduction

3.1.1 Background

Various studies show that localization of a sound can be influenced by preceding auditory stimuli. Changes in localization can occur on very short time scales (milliseconds), for example those related to the precedence effect [71], in which perceived spatial position of a target is shifted towards immediately preceding sound, or longer time scales (seconds to minutes), observed when subject is exposed to prolonged adapting sound and perceived position of subsequent targets is shifted away from adaptor’s position [24][25][26][78].

Effect of preceding distractor on localization of a target was also studied by Kopčo et al. [64]. As expected, distractor affected localization of subsequent target, but in addition, another effect was observed, which authors referred to as “contextual plasticity” and which caused that responses on interleaved control trials, in which the target was presented alone without any preceding distractor, differed depending on whether the control trials were presented in context of trials with frontal or with lateral distractor. In other words, even though the target was not immediately preceded by any distractor, its localization was affected by the context of other trials (with distractor).

To our knowledge, no such contextual plasticity has been observed in other sound localization studies so far. In following sub-chapters, we will describe Kopčo et al. study [64] in more detail and we will try to relate it to other studies of plasticity.

3.1.2 Contextual plasticity observed in preceding study

Kopčo et al. study [64] was designed to examine the effect of immediately preceding distractor on localization of a target sound.

Subject was surrounded by arc of 9 loudspeakers, equally spaced on a quarter-circle. The distractor was fixed at either frontal or lateral location during an experimental run, while targets were presented randomly from each of the seven middle loudspeakers.

Experimental run consisted of 1) test trials in which two stimuli were presented: first distractor, then target, with various stimulus-onset asynchronies (SOAs: 25, 50, 100, 200, or 400 ms), and of 2) control trials in which the target was presented alone. These two types of trials were randomly interleaved within experimental run.

Subject's task in each trial was to localize a target and ignore the distractor if present. Figure 1 shows mean localization responses for runs with frontal distractor (panel A) and runs with lateral distractor (panel B). As authors expected, localization of target in test trials was biased due to preceding distractor (compare solid line and dashed line in each panel of Figure 1). But unexpectedly, responses on control trials which were meant to be a reference not affected by distractor, differed when presented in context of test trials with frontal versus lateral distractor (compare dashed lines for identical actual target locations in panel A versus panel B in Figure 1). For frontal distractor, responses were biased more laterally than for lateral distractor. These results suggest that context of trials with distractor affected responses also on interleaved control trials. Authors referred to this effect as „contextual plasticity".

Since the experiment did not include any run consisting exclusively of no-distractor trials, the magnitude of the effect caused by presence of distractor trials within a run could not be computed. However, it was possible to assess the effect of a change in location of the distractor (i.e., a change in context instead of presence of context), by computing the difference between responses for frontal versus lateral distractor.

The contextual effect computed this way had a magnitude of approx. 6° or 9°, depending on the type of environment (classroom/anechoic) and was roughly independent of target laterality (Figure 2A).

To examine the build-up of the contextual effect, the time course of experimental run was divided into 4 balanced parts, which represented 4 repeats of each combination of target location and SOA condition (including no-distractor). Contextual bias built up within 3 subruns (Figure 2B), which might represent approx 3-4 minutes (taking into account that the experimental run lasted approx. 5 minutes).

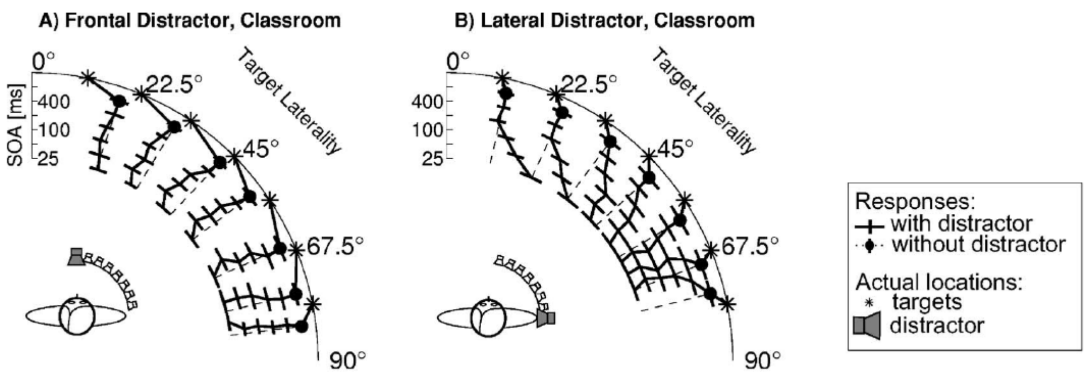

Figure 1 Mean localization responses from Kopčo et al. [64], for frontal-distractor condition (panel A) and lateral-distractor condition (panel B). Each panel shows across-subject mean and standard error in perceived target lateral angle as a function of target lateral angle for trials with distractor (with various SOAs) and for trials without distractor. (Reprinted from Kopčo et al. [64], with permission of the first author).

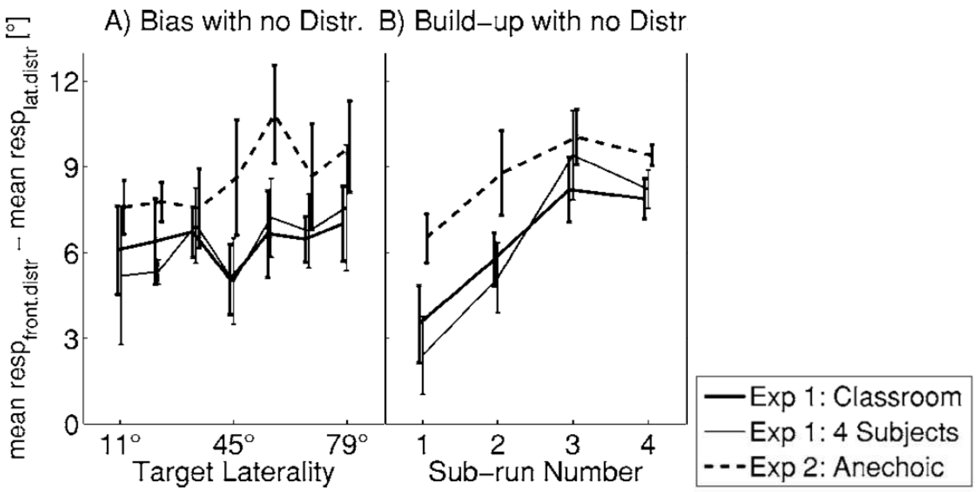

Figure 2 Contextual bias from Kopčo et al. [64] computed as a difference between responses on control trials in context of frontal vs lateral distractor, plotted as a function of target location (panel A) or averaged across target laterality and plotted as a function of subrun within experimental run (panel B). Across-subject mean and within-subject standard error of the mean are plotted. Contextual effect is shown as a function of target location relative to subject's frontal median plane. Solid lines show data for echoic environment (classroom) and dashed line shows data for anechoic environment (Reprinted from Kopčo et al. [64], with permission of the first author).

Several interpretations of this effect were suggested, for example, that it is a bottom-up process driven by statistical distribution of the stimuli (45% of the stimuli within a run were presented from a fixed distractor location) or that it is a top-down process such that the listener focuses his/her attention away from the (a priori known) distractor location in order to better localize the target. However, the absence of a baseline of only no-distractor trials, relative to which the effect could be evaluated, did not allow to examine the effect more detailedly. In addition to the question of whether it is a bottom-up or a top-down process, many other questions can be posed in order to understand the cause of the effect and its properties. In this thesis we will focus on the questions stated below.

3.1.3 Problems and Hypotheses

It is not known why the contextual effect observed in [64] occurs, or how it is related to other already known examples of short-term plasticity in sound localization such as the one induced by misleading visual feedback [22][23], by training with misaligned audiovisual stimuli (i.e., ventriloquism aftereffect [10]), or prolonged exposure to adapting sound [24][25][26][78] (for more details see chapter 2.2.2 Studies of plasticity). Several aspects of the effect need to be studied in order to understand it. In the thesis we will focus on its spatial aspects which help to reveal the explanation of the effect as well as its underlying neural representation. We proposed two sets of hypotheses based on two different views of the contextual effect which were examined in separate experiments.

3.1.3.1 Hypotheses for Experiment 1: Contextual effect as a change in strategy

One of the possible explanations of the contextual effect is that it arises from how subjects localize targets in distractor trials. Specifically, in distractor trials, the interval between the distractor and subsequent target is very short, resembling conditions of the precedence effect, in which the spatial information about the sound is degraded by immediately preceding sound (see subchapter 2.1.5.1 Precedence effect). In order to localize the target properly, subjects might focus their attention away from a priori known location of the distractor (or try to compensate for the fact that the perceived location of the target is shifted towards the distractor). Hence they shift their responses away from the distractor location against the shift caused by the precedence effect. Subjects might use this strategy within whole experimental run, including also the interleaved no-distractor trials, because they didn't know in advance what type of trial (distractor/no-distractor) will follow. Based on this explanation we formulated three hypotheses:

Since it is more difficult to distinguish between the two sound sources if they are close to each other, more effort would be required to localize a target closer to the distractor than to localize a target farther away from the distractor. Hence, it can be expected that: **Hypothesis H1a: Contextual bias will be larger when distractor-targets are presented near the distractor, compared to when they are presented farther away from the distractor.**

If the contextual effect arises from an effort to separate distractor location from possible target locations, presenting distractor targets on both sides of the distractor within one run would result in smaller or no contextual bias, because subject would not know in advance in which direction to focus (i.e., to which direction "repel" the target to move it perceptually away from the distractor) in order to counteract the precedence effect. Hence, another hypothesis can be stated: **H1b: No contextual effect will be observed when targets in distractor trials will be presented on both sides of the distractor.**

The final hypothesis was related to the fact that auditory spatial resolution worsens with increasing laterality (see sub-chapter 2.1.7 Accuracy of sound localization). Precedence effect studies also report the dependency of the effect on azimuth, showing worse discrimination of the lagging sound relative to lead location when the leading and lagging sounds are located at more lateral locations [91]. Since more effort seems to be required when the two stimuli originate from lateral, compared to frontal, locations, we hypothesize that: **H1c: Contextual effect will increase with increasing angular distance of the distractor relative to straight ahead.**

To test these hypotheses, we designed an experiment (Experiment 1) with setup similar to that in [64], except that in addition to existing distractor locations 0° and 90° relative to subjects frontal median plane, we added one more at 45°, and we restricted the presentation of targets in distractor trials to locations either to the left, to the right, or to both sides off the central speaker.

3.1.3.2 Hypotheses for Experiment 2: Possible neural representation of the contextual effect

In hypotheses in this section we focused on examining the possible underlying neural representation of the effect, which can link it either to earlier or later stages of sound localization processing. Similarly to hypotheses in a previous section, hypotheses in this section were tested by examining spatial aspects of the contextual effect.

We assumed that the contextual effect is associated with changes in a topographically organized auditory map such that the distractor trials will induce shift in the map in the direction “from distractor towards distractor trials”. We will consider that the effect operates on two underlying representations, each associated with different stage of sound localization processing. We will refer to them as “polar” and “Cartesian” in order to distinguish whether they are symmetric relative to the specific point (pole) or not, but not referring to other aspects from mathematical definitions of these terms.

Polar representation (with poles at azimuths +-90°) is associated with earlier stages of localization processing, such as ITD/ILD processing in MSO/LSO. This stage of processing is characterized by the fact that the values of localization cues are the same for locations symmetric relative to interaural axis and hence they activate identical groups of neurons. On the other hand, Cartesian representation is associated with later stages of processing, after the different localization cues are integrated (for example IC or cortical level). In Cartesian representation, each location around the listener is represented by different group of neurons, i.e., locations behind the interaural axis are coded separately from locations in front of the interaural axis.

To address the question of on which of the two representations the contextual effect operates, we need to examine whether the effect induced on one side of the interaural axis (hypothetical pole) generalizes to same extent and with opposite direction also to symmetrical locations at the other side interaural axis (i.e., such that responses on both sides of the distractor placed at interaural axis would be shifted away from the distractor) – this would indicate polar representation, or whether the shift will be in same direction (similarly to shifts induced by visual stimuli in Kopčo et al. [79]) – this would indicate Cartesian representation.

Another spatial aspect of the effect according to which the two representations can be distinguished is how will the contextual bias look like when we induce it on both sides of the distractor placed at interaural axis (i.e., as if we induced two biases against each other). No bias observed would indicate Cartesian representation, since contextual bias from opposite sides would cancel out. On the other hand, if the bias will be similar (or even larger) to bias observed for context on one side of the distractor, it would indicate polar representation, since distractor targets from opposite sides would affect same neural population, what will only strengthen inducement of the contextual effect.

Previous predictions are valid only when the region around the pole (in this case interaural axis) is examined. When the tested region of space does not cross any pole, the polar representation should result in the same contextual bias as a Cartesian representation. Hence, when bias is induced on one side of the distractor, the locations at which no bias was induced should be shifted in the same direction as locations at which the bias was induced. And, when bias is induced on both sides of the distractor, it should lead to cancellation of the contextual bias.

To test these hypotheses, we designed an experiment, in which we placed the distractor to the center of the speaker array and we restricted the presentation of targets in distractor trials (i.e., context) to locations on one side of the distractor (left/right), or to both sides of the distractor. These spatial configurations were tested either for speaker array placed around the interaural axis (lateral orientation), or around frontal median plane (frontal orientation). Expectations for such setup are summarized in Figure 3.

We hypothesize that the effect occurs at later stages of processing and hence that it is based on Cartesian representation. This leads to following predictions:

H2a: Context presented on one side of the distractor will shift all locations in the same direction, for both orientations of speaker array relative to subject.

H2b: Context presented on both sides of the distractor will induce no contextual bias, since biases from opposite sides will cancel out. This will be also valid for both orientations of speaker array relative to subject.

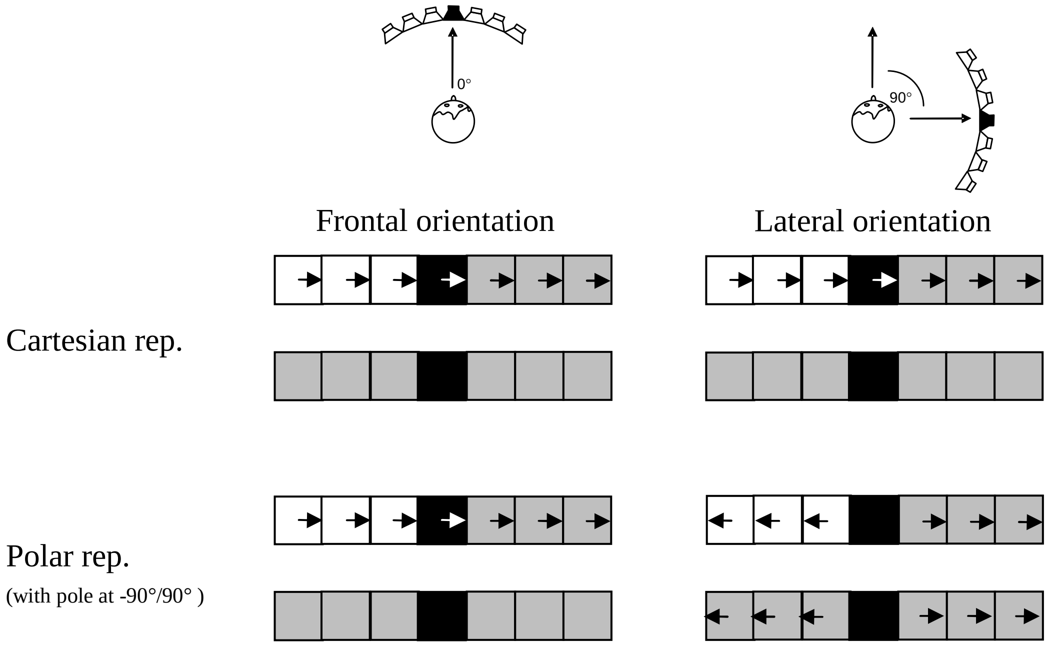

Figure 3 Schema of the expected effect of the context for the two considered underlying neural representations (Cartesian and polar), for each combination of orientation of tested spatial region relative to subject (frontal; lateral), and context spatial configuration (on one side off the distractor; on both sides off the distractor). Blocks indicate target locations. Grey blocks represent locations in which also the distractor-targets were presented (i.e., context locations), black blocks indicate distractor locations. Arrows show expected direction of the bias (if no arrow is present, no bias is expected).

In the experiment, we also considered the fact that spatial resolution is better at frontal locations compared to lateral locations (see chapter 2.1.7 Accuracy of sound localization) and if contextual effect operates on such representation in which the space is not uniformly represented, we might observe different contextual effects for these two regions. Specifically, broader receptive fields at more lateral locations (if they span region larger than covering only one target location) could be affected more in comparison to narrower receptive fields at frontal locations, due to the fact that more distractor-targets fall within the receptive field. Hence, we hypothesize that:

H2c: Lateral distractor will induce stronger contextual bias than frontal distractor.

3.2 Experiment 1

3.2.1 Methods

3.2.1.1 Subjects

Eight normal-hearing subjects (7 males, 1 female) aged 23-29 participated in the experiment.

3.2.1.2 Setup

Experiment was performed in a dark semi-anechoic booth of 3 x 2 x 3 m (length x width x height). Subject was seated in the center of a quarter circle of 9 loudspeakers (i.e., separated by 11.25° step) positioned at 1.5m height, 1.1 m away from subject (Figure 4). Speakers were hidden behind acoustic cloth.

Sound stimuli were presented using soundcard Fireface 400 and amplified by Crown D75-A amplifier.

A hand-held pointer was used to indicate perceived sound position. Responses were acquired using video system, which captured the coordinates of speakers, head and pointer after subject pressed a button on a hand-held pointer. The coordinates were transformed to angular bias relative to actual target location.

Experimental procedure for presentation of the stimuli and data collection was written in MATLAB. This environment was also used for data analyses and visualization.

3.2.1.3 Task

Subject's task was to localize a target sound by pointing to a perceived location of the target using hand-held pointer. On some trials (i.e., distractor trials) the target was preceded by the distractor which should be ignored. Subjects were instructed to have their eyes closed to avoid possible visual feedback and not to move their head during an experimental run.

3.2.1.4 Stimuli and types of trials

All stimuli used in the experiment (distractor sound and target sound) were identical 2-miliseconds-long frozen noise bursts. Similar experimental design as in

Kopčo et al. [64], in which the contextual effect was observed, was created. Two types of trials were used in an experiment:

- **No-distractor trials** – consisted of target sound, which was presented from one of the 7 possible target locations.
- **Distractor trials** – consisted of distractor followed by target sound, with distractor-to-target onset asynchrony of 25 ms. Distractor location was fixed within a run and could be either frontal (D0; located at 0° relative to the listener), intermediate (D45; located at ±45° relative to the listener) and lateral (D90; located at ±90° relative to the listener). Target in distractor trials (further referred to as "distractor-target") could come from one of the speakers defined by context configuration, which was fixed within a run (three left-most target speakers, three right-most target speakers, or both).

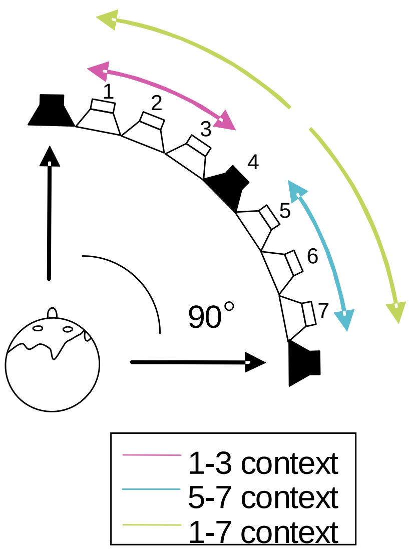

Figure 4 Experimental setup. Black arrows indicate two possible subject orientations relative to the speaker array. Filled loudspeakers represent possible distractor locations: frontal (0°), intermediate (45°), and lateral (90°), while only one of them is used as a distractor in a particular run. Labeled loudspeakers indicate possible target locations (including speaker 4, which in case of intermediate distractor condition is used for presenting both distractor and target stimuli). In distractor trials, targets are restricted to three context configurations, depicted by arrows above the speaker array: speakers {1,2,3}, {5,6,7}, or {1,2,3,5,6,7}

3.2.1.5 Procedure

Experiment was structured into four approx. 1.5-hour long sessions, each consisting of two types of runs (see Figure 5, Figure 6). In **distractor runs**, distractor and no-distractor trials were randomly interleaved, similarly to Kopčo et al. [64]. In addition to Kopčo et al. [64], which did not have any reference according to which a size of the contextual effect could be estimated, here a „**baseline run**" consisting of no-distractor trials only was also included.

Both types of runs consisted of 210 trials. Distractor runs were divided into pre-adaptation- (14 trials), adaptation- (168 trials) and post-adaptation (28 trials) part. Contextual effect was induced (i.e., distractor trials were presented) only in adaptation part, while pre- and post-adaptation part contained only no-distractor trials, to study how plasticity built up after the context onset and decayed after the context offset (see Figure 5). In adaptation part, distractor trials were randomly interleaved with no-distractor trials (75% of distractor trials, 25% of no-distractor trials).

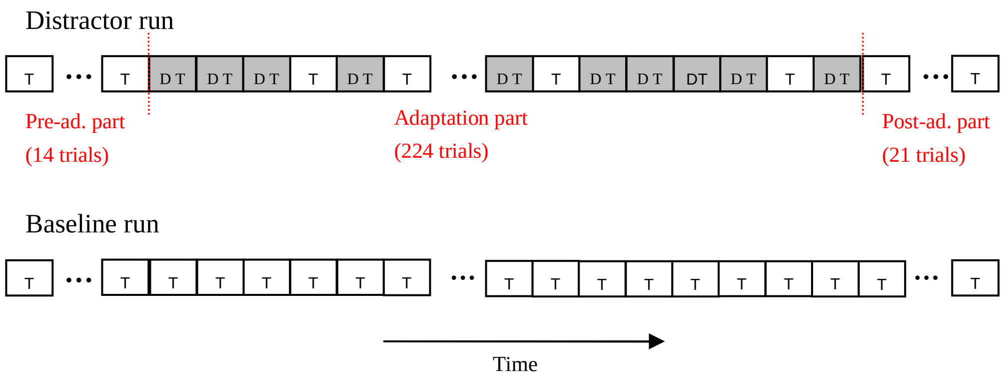

Figure 5 Schematic view of types of runs used in the experiment. Each small block represent one trial, either distractor trial (grey „DT" block, denoting presentation of distractor followed by target sound), or no-distractor trials („T" block, denoting presentation of target sound only). Distractor runs consists of both distractor trials and no-distractor trials, randomly interleaved, while baseline run consists of no-distractor trials only. To analyze the contextual effect, we consider only no-distractor trials (i.e., „T" blocks) from each run. Adaptation part of the distractor run (within interval denoted by red dashed line), which contained both distractor- and no-distarctor trials, is preceded and followed by no-distractor trials only (14 pre-adaptation trials, and 28 post-adaptation trials) to allow analysis of build-up and decay of adaptation.

To distribute target locations uniformly in time, locations of targets within a run varied pseudorandomly, specifically as a sequence of permutations of all possible target locations (separately for distractor and no-distractor trials). To analyze the time course of adaptation, run was divided into smaller parts called subruns, representing repeated presentations of the target from specific location. Since the analysis is primarily focused on no-distractor trials, the number of subruns was also determined by repeats of no-distractor targets. However, the total number of no-distractor targets differed between distractor runs and baseline. In order to unify them, we chose fixed number of subruns shared for both types of runs. The number was based on number of repeats in distractor runs. Repeats within no-distractor run were uniformly distributed among these bins such that the temporal order was not violated and values within each bin were averaged.

To examine the spatial aspects of contextual plasticity, we restricted the locations from which targets in distractor trials could be presented (i.e., we changed the spatial distribution of the context). Three **context configurations** were used (for speakers ordered from left to right; see Figure 11):

- 1-3 context: context restricted to speakers 1,2,3
- 5-7 context: context restricted to speakers 5,6,7
- 1-7 context: context restricted to speakers 1-3 and 5-7 (label „1-7 context“ was used instead of „1-3 & 5-7 context“ for simplification).

Locations to which the context is restricted in a particular run will be referred to as “on-context locations” (locations 1-3 for 1-3 context, 5-7 for 5-7 context), while the remaining target locations will be referred to as “off-context locations” (locations 5-7 for 1-3 context and 1-3 for 5-7 context).

We also manipulated the **location of the distractor** relative to subject’s frontal median plane (i.e., relative to straight ahead) using three possible locations: 0°, 45°, or 90° (i.e., frontal, intermediate, or lateral distractor, respectively).

In order to test localization in both hemifields, we manipulated also the **orientation** of the subject relative to the speaker array, using either orientation towards left-most speaker (all target locations to the right of the listener), or towards the right-most speaker (all target locations to the left of the listener).

Context configuration, distractor location and subject’s orientation were fixed within a run.

Taken together, there were 20 types of runs in the experiment: 2 orientations (left/right) x [3 distractor locations (0°, 45°, 90°) x 3 context configurations (1-3 context, 5-7 context, 1-7 context) + baseline run].

Experiment was structured into 6 sessions. Each session consisted of 10 runs, including all combinations of distractor location and context configuration, and baseline. Orientation changed after each run within a session, such that possibly induced perceptual changes on underlying spatial representation would not transfer between successive runs.

Experiment was balanced such that each type of run was presented equal number of times. Structure of the experiment is summarized in Figure 5 and Figure 6.

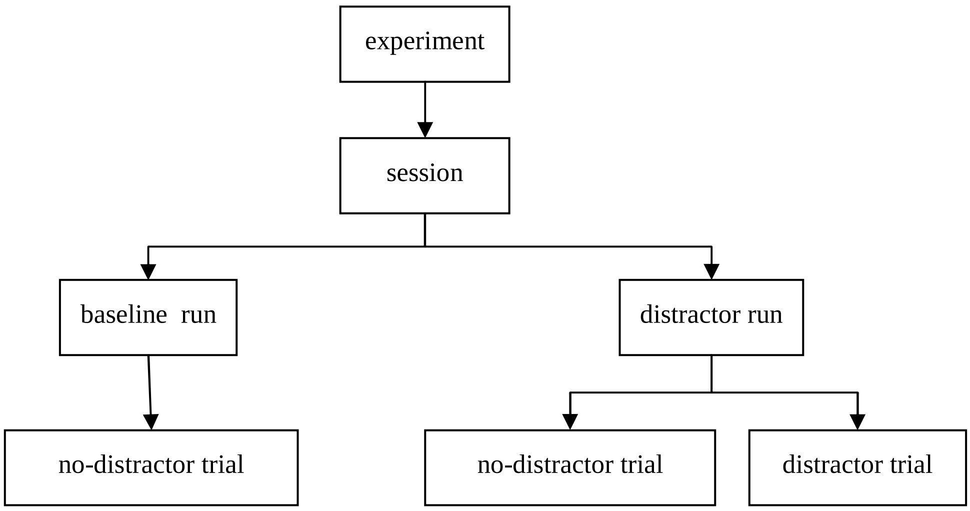

Figure 6 Schematic view of the experiment structure depicted as a breakdown of higher structural blocks into smaller structural blocks. Experiment consists of sessions. Sessions consist of runs of two types: baseline and distractor run. Runs consist of trials, either of only no-distractor trials (a baseline run), or both no-distractor trials and distractor trials (a distractor run).

Before each run, subject was informed about conditions in following run (orientation relative to the speaker array, location of the distractor, type of the run – distractor/baseline, context configuration). Reference signs were placed in the room for the two orientations to help subjects properly orient their seat according to instructed orientation.

3.2.1.6 Data analysis

Before any analyses, data were statistically preprocessed. A median was computed from all responses satisfying specific combination of conditions (context configuration, distractor location, orientation, trial type (distractor / no-distractor, target location)). All responses from this group which were more than 20° apart from the median (to either side) were considered as outliers and excluded from further analysis. Moreover, data known to be associated with technical errors were also excluded. Overall, excluded data represented approx. 3% of all data (when pooled across all conditions and subjects).

Responses for the two subject’s orientations relative to the speaker array were approximately symmetrical, therefore the data for subject facing right-most speaker were mirror-flipped and averaged with data for subject facing left-most speaker. If not specified differently in graphs, all analyses are performed on these averaged data.

For the analysis of the contextual effect, only no-distractor trials were considered from both types of run. By the term „contextual effect“ we will refer to difference between responses on no-distractor trials from adaptation part of distractor runs (supposed to be affected by context of interleaved distractor trials presented within a run) and responses in baseline run, see Figure 5. If not specified differently, only subruns 4-8 are considered (instead of 3-8 representing whole adaptation part), because the contextual bias might require time to build up.

All figures (if not specified differently) show across-subject mean and across-subject standard error of the mean. Target locations in the figures are labeled by numbers 1-7 representing azimuths 11.25° – 78.75°, with 11.25° step.

Data were subjected to repeated measures analysis of variance (further in the text only referred to as ANOVA), and Box-Geisser-Greenhouse correction was applied. We report uncorrected degrees of freedom for F-values and corrected p-values.

3.2.2 Results

Before analysis of the contextual effect, we will describe localization in general, i.e., compare responses with actual target locations (Figure 7) for each of the three distractor locations (depicted by triangle above the x axis).

In baseline run (orange line), subjects tended to shift their responses towards the center of the response range (positive bias for target locations #1-3 and negative bias for locations #5-7). This effect can be given for example by the fact that subjects were aware of a possible range of responses, and, if unsure about target location, rather responded towards the center of the range than away from it. Responses tend to be skewed also in conditions with context (pink, blue and yellow lines have negative slope). Similarly to [64], context of distractor trials affected interleaved no-distractor responses, which can be observed either by comparing responses for the different distractor locations (similarly to how contextual effect was computed in [64]; compare lines of the same color between the three panels) or comparing responses in context conditions relative to baseline condition (how the contextual effect will be computed in current study; in each panel compare pink, yellow and blue lines with orange line).

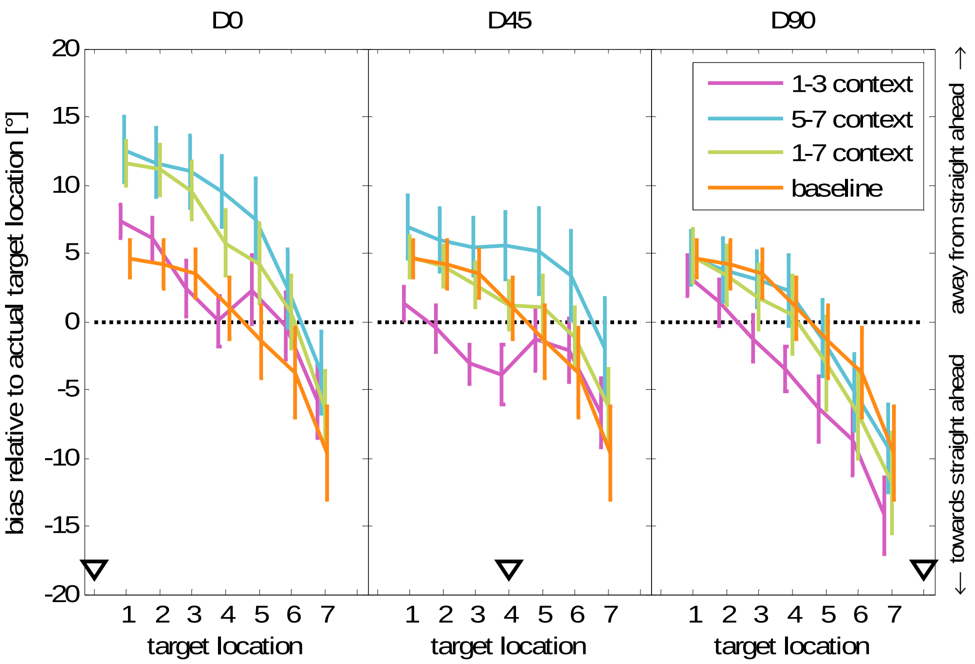

Figure 7 Bias relative to actual target location as a function of target location. Three panels show data separately for each distractor location: frontal, intermediate and lateral (panels from left to right, respectively). Distractor location is indicated by triangle above x-axis.

In order to verify whether the contextual effect observed here is similar to what was observed in [64], the difference between responses in context of frontal vs. lateral distractor is plotted and compared to analogous figure from previous study [64] (Figure 8; compare solid lines in both figures). The magnitude of the difference is roughly around 7°, which is similar to what was observed in [64]. The spatial pattern of the observed effect is also very similar between the two studies, suggesting that they are describing the same phenomenon. The difference is in both figures positive, what indicates that no-distractor-trial responses in context of frontal distractor are relatively farther from straight ahead than no-distractor-trial responses in context of lateral distractor. However, effect computed this way does not specify how the presence of the context affects responses compared to "normal localization".

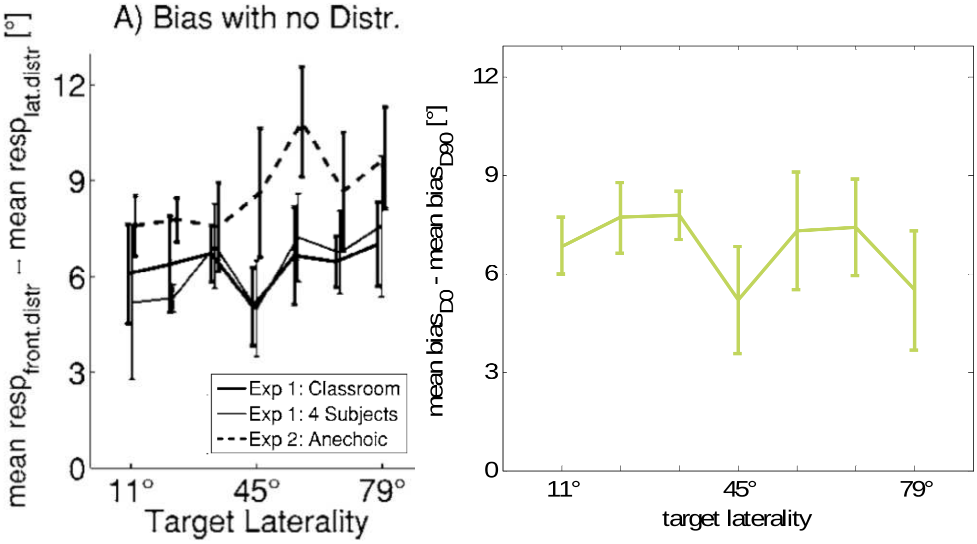

Figure 8 Contextual bias computed as a difference between responses on no-distractor trials in context of frontal vs lateral distractor, from Kopčo et al. study [64] (panel A, reprinted from Kopčo et al. [64], with permission of the first author) and from current study (panel B). Across-subject mean and within-subject (panel A) or across-subject (panel B) standard error of the mean are plotted. Data from current study are comparable to solid lines from [64].

To analyze the effect relative to normal localization, we computed the difference between no-distractor-trial responses "with context" and responses of "normal localization" in baseline condition (Figure 9). For all distractor locations and all context configurations, context induced bias away from the distractor. The magnitude of the contextual bias and its spatial pattern differed between the conditions.

For **intermediate distractor** (central panel), context on both sides of the distractor (yellow line) induced no (target locations 1-3) or only small (target locations 5-7) contextual bias away from the distractor. This bias was not significantly different from baseline condition. Context only on one side of the distractor induced bias of up to approx. 7° at on-context locations (locations 1-3 for pink line and 5-7 for blue line), which generalized also to neighboring location 4, while almost no contextual bias was observed at other off-context locations.

For **frontal distractor** (left panel), 1-7 context (yellow line) induced bias of approx. 7°, which decreased with increasing angular distance from the distractor. Context presented only on near locations (pink line) or far locations (blue line) induced bias with more complicated spatial pattern (described later in the section), however, when the bias is compared to bias in 1-7 context condition, the pattern is more clear: at off-context locations, the responses are the same as in 1-7 context, but at on-context locations and neighboring location 4, the responses are shifted relative to 1-7 context condition towards the side at which the distractor targets were presented (pink line separates from yellow line at locations 1-4 and blue line separates from yellow at locations 4-7). It results into overally smaller contextual bias induced by near-context compared to far-context.

Similar pattern of contextual bias, even though smaller in magnitude, than for frontal distractor was observed also for the **lateral distractor** (right panel), with 1-7 context causing contextual bias largest near the distractor location and decreasing with increasing distance away from the distractor and with the two half-range context conditions separating from the whole-range context condition (note that since the distractor was at the opposite side, near-context condition is now represented by blue line and far-context by pink line). The separation is smaller than for frontal distractor, since even 1-7 context condition induced much smaller bias.

In order to compare the effect of the distractor location on contextual bias, we will consider only distractor locations D0 and D90. We excluded condition D45 due to the fact that different region relative to the distractor location was examined than for D0 and D90 conditions (region to both sides of the distractor compared to larger region only on one side of the distractor), and this might have influenced the contextual bias. Larger bias was observed for frontal distractor than for lateral distractor.

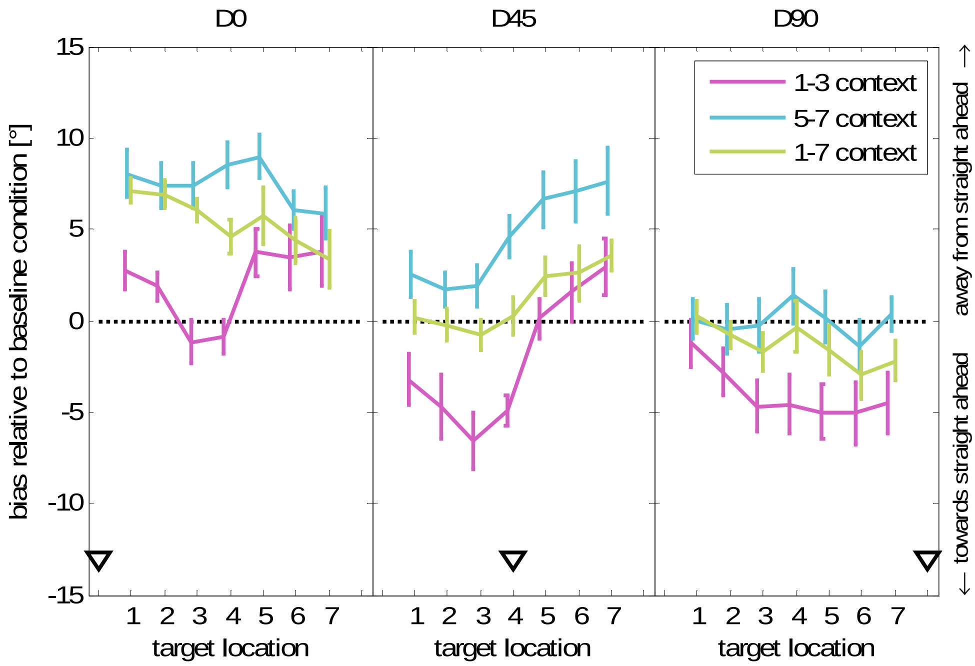

Figure 9 Contextual bias computed as a difference between responses on no-distractor trials in distractor runs versus responses in baseline, plotted as a function of actual target location (relative to straight ahead). The three panels show a condition with frontal distractor (panel A), intermediate distractor (panel B) and lateral distractor (panel C). Distractor location is indicated by a triangle above x-axis.

Since the spatial pattern of the contextual bias was similar for frontal and lateral distractor conditions, we averaged the data across the two conditions (Figure 10). When context was presented near the distractor (pink line), the magnitude of the effect was generally very small (less than 2°). A tendency towards a specific spatial pattern can be observed: the responses to targets closest to the distractor were shifted away from distractor and the shift decreased with increasing distance of the target from the distractor. At off-context locations the contextual bias again rises to approx. 2° and is constant for all off-context locations. However, due to the small magnitude of the biases for this condition and large standard errors of the mean, this spatial pattern is doubtful.

When context was presented far from the distractor (blue line), the magnitude of the bias was higher than for near-context condition. At off-context locations, it was approx. 7° (and again, constant), and at on-context locations it decreased with increasing distance from the distractor to approx. 4°.

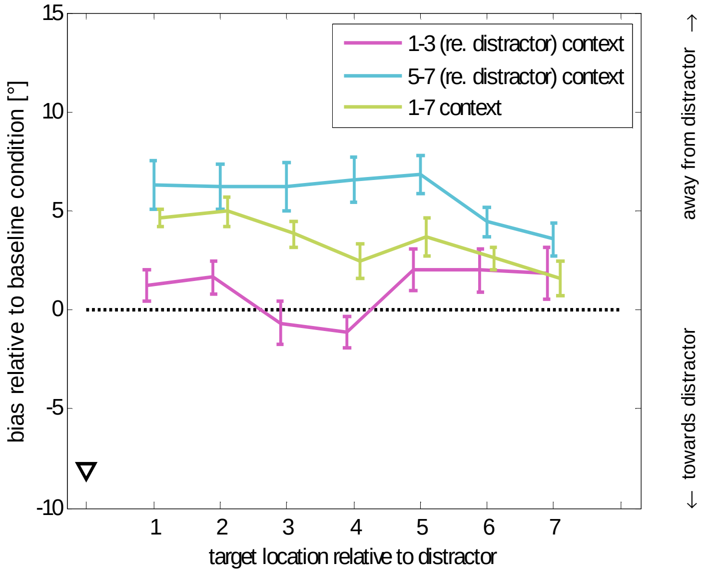

Figure 10 Contextual bias as a function of target location relative to distractor (increasing numbers indicate increasing distance from the distractor), averaged across frontal-distractor- and lateral-distractor condition. The three lines show three context configurations: with context near the distractor (pink line), far from the distractor (blue line), or both (yellow line).

Data were subject to repeated-measures ANOVA with factors of context (3 distractor locations × 3 context configurations + baseline) and target location (1-7), which revealed significant main effect of context ($F_{9,63}$=16.73, p<0.01), significant main effect of target location ($F_{6,42}$=16.10, p<0.01) and significant interaction between context and target location ($F_{54,378}$=6.58, p<0.01). Significance of a target location factor points to centrally "skewed" responses already discussed before. Significant main effect of context confirms that context affects responses. Pairwise comparisons between the "baseline" level and other levels of the factor context found that following levels significantly differ from baseline condition: D0:5-7 context (blue line in left panel of Figure 7); D0:1-7 context (yellow line in left panel of Figure 7) and D45:5-7 context (blue line in central panel of Figure 7). No difference between D45:1-7 context and baseline was found, what suggests that when context was on both sides of the distractor, no bias was induced. Significant interaction between context and target location supports already mentioned observation that different types of the context lead to different spatial patterns of responses.

In order to compare the contextual biases induced by different types of context, ANOVA was performed also on data in a form of a contextual bias (as in Figure 10, but separately for each distractor location), with factors of distractor location (D0, D90), context configuration relative to distractor (1-3 context, 5-7 context, 1-7 context) and target location relative to the distractor (1-7). Significant main effect of context configuration ($F_{2,14}$=11.66, $p<0.01$) and main effect of distractor location ($F_{1,7}$=7.55, $p<0.05$), and significant context configuration × target location interaction ($F_{12,84}$=4.82, $p<0.01$) was found. Significant main effect of context configuration suggests that far-context configuration induced larger bias than near-context configuration. Significant main effect of distractor location suggests that the contextual bias was larger for frontal distractor compared to lateral distractor. Significant interaction between the context configuration and target location shows that different context configurations induced different spatial patterns of contextual bias.

3.2.3 Discussion

The context of distractor trials induced a bias in responses on interleaved no-distractor trials, similar to bias observed in previous study [64]. Here we provided a baseline run as a reference, which allowed comparison of responses relative to “normal localization”. It was found that the context of distractor trials causes bias in responses away from the distractor. The contextual bias generalizes from the region in which it was induced also to other locations, but the pattern of the generalization is not constant across all target locations (as a simple shift of the spatial map) but has more complicated spatial pattern. The generalization of the effect to locations between the distractor and the distractor-targets is clear, however, the generalization from near-distractor locations to farther locations is doubtful due to overally small magnitude of the effect and large standard errors in the mean biases.

In hypothesis H1a, we predicted that the contextual bias will be larger when distractor-targets are presented near the distractor, compared to when they are presented farther away from the distractor. The location of the distractor-targets affected the contextual bias, but contrary to H1, the near-context tended to induce smaller bias than far-context.

Hypothesis H1b predicted that no contextual effect will be observed when targets in distractor trials will be presented on both sides of the distractor. The results were consistent with this hypothesis.

Hypothesis H1c predicted that the contextual bias will increase with increasing angular distance of the distractor relative to straight ahead. This hypothesis was not confirmed, since the lateral distractor caused the smallest biases among the possible distractor locations.

Interestingly, the largest bias (when only near-distractor context configuration is considered) could be observed for the intermediate distractor. The reason for this effect is not clear. However, intermediate distractor condition differed from the frontal and the lateral distractor conditions not only by location of the distractor relative to subject's straight ahead, but also by location of the distractor relative to the speaker array. For frontal and lateral distractor conditions, the distractor was at the side of the array, while for intermediate distractor location, the distractor was at the center of the array. While with distractor at the center of the array, the space could „stretch" freely to the side, with distractor at side the stretching might be counteracted by presenting only the no-distractor targets at locations farther away from the distractor.

In summary, the results are in some aspects not consistent with proposed explanation of the contextual effect based on listener's localization strategy and alternative explanations need to be considered (The alternative explanations will be discussed after also the data from the Experiment 2 are analyzed).

3.3 Experiment 2

In this experiment, we will examine possible neural representation of the contextual effect.

3.3.1 Methods

If not specified differently in subsequent sections, same methods as in experiment 1 are used.

3.3.1.1 Subjects

Ten normal-hearing subjects (8 males, 2 females) participated in the experiment. Their age ranged from 21 to 28 years.

3.3.1.2 Setup

Experimental setup is the same as in the Experiment 1 except that two side-most speakers are not used in this experiment, i.e., speaker array spans an area of 67.5°

(Figure 11). In current experiment, distractor is always in the middle of the speaker array, while possible target locations and context configurations remain the same as in Experiment 1.

3.3.1.3 Procedure

Experiment was structured into four approx. 1.5-hour long sessions consisting of distractor runs and baseline run. Both types of runs consisted of 259 trials. Distractor runs were divided into pre-adaptation- (14 trials), adaptation- (224 trials) and post-adaptation (21 trials) part.

The same three **context configurations** as in Experiment 1 were used (for speakers ordered from left to right; see Figure 11):

- 1-3 context: context restricted to speakers 1,2,3
- 5-7 context: context restricted to speakers 5,6,7
- 1-7 context: context restricted to speakers 1-3 and 5-7 (label „1-7 context“ was used instead of „1-3 & 5-7 context“ for simplification)

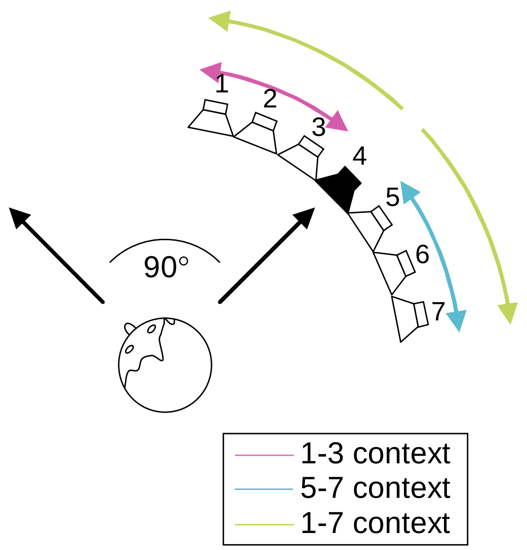

Figure 11 Experimental setup. Distractor position is indicated by filled loudspeaker. Labeled loudspeakers indicate possible target locations (note that speaker 4 is used as a distractor and also as a target). Black arrows indicate two possible subject orientations re. speaker array (medial or lateral, while only one of the lateral orientations is shown). Arrows above the speaker array show 3 possible context configurations, which represent locations from which targets in distractor trials are presented: speakers {1,2,3}, {5,6,7}, or {1,2,3,5,6,7}.

To examine whether contextual plasticity operates on such representation in which the space is non-uniform, we varied also orientation of the speaker array relative to the subject: medial (0°) vs. lateral (-90° or 90°), see Figure 11.

Context configuration and subject's orientation were fixed within a run.

Taken together, there were 12 types of runs in the experiment: 3 orientations (0°/-90°/90°) x [3 context configurations (1-3 context, 5-7 context, 1-7 context) + baseline run].

Within each session, only 2 orientations were used (frontal and one of the lateral orientations) resulting into 8 types of runs within session (2 orientations x [3 context configurations + baseline]) Orientation within session changed from run to run. Also lateral orientation -90° and 90° changed from session to session.

Before each run, subject was informed about conditions in following run (orientation relative to the speaker array, type of the run (distractor, no-distractor), context configuration (left half of the array, right half of the array, whole array)). Reference signs were placed in the room for all 3 orientations to help subjects properly orient their seat according to actual orientation.

3.3.1.4 Data analysis

No outliers were excluded from the data except for errors due to technical problems (approx. 0.06% of all data). Responses in condition with two lateral orientations (-90° and 90°) were approximately symmetrical, therefore the data for subject's orientation to the right of the distractor were mirror-flipped and averaged with data for subject's orientation to the left. If not specified differently in graphs, all analyses are performed on these averaged data.

If not specified differently, only subruns 4-10 are considered (instead of 3-10 representing whole adaptation part), because the contextual bias might require time to build up.

All figures show across-subject mean and across-subject standard error of the mean.

Data were subjected to repeated measures ANOVA. Box-Geisser-Greenhouse correction was used, which adjusted degrees of freedom. We report uncorrected degrees of freedom for F-values and corrected p-values.

3.3.2 Results

Figure 12 shows responses relative to actual target locations. Responses in baseline tend to be slightly shifted towards the center of the speaker array (note positive bias for locations to the left of the distractor and negative bias for locations to the right of the distractor), similarly as in Experiment 1. Responses in context conditions tend to follow this trend, but in addition they are altered due to specific context configuration. This shift towards the center of the speaker array is more pronounced for lateral orientation, especially for targets behind interaural axis (see negative bias for target locations #5-7 in the right panel of Figure 12). Large bias for targets behind interaural axis is most probably caused by increased front-back confusions, or by method of responding (more effort required to point behind interaural axis). However, differences between context conditions are similar for both orientations, suggesting that the bias for targets behind lateral axis does not influence how these responses were affected by context. In other words, even though the pattern of responses does not perfectly correspond with actual target locations and is rather skewed for lateral orientation, we can analyze the contextual effect independently.

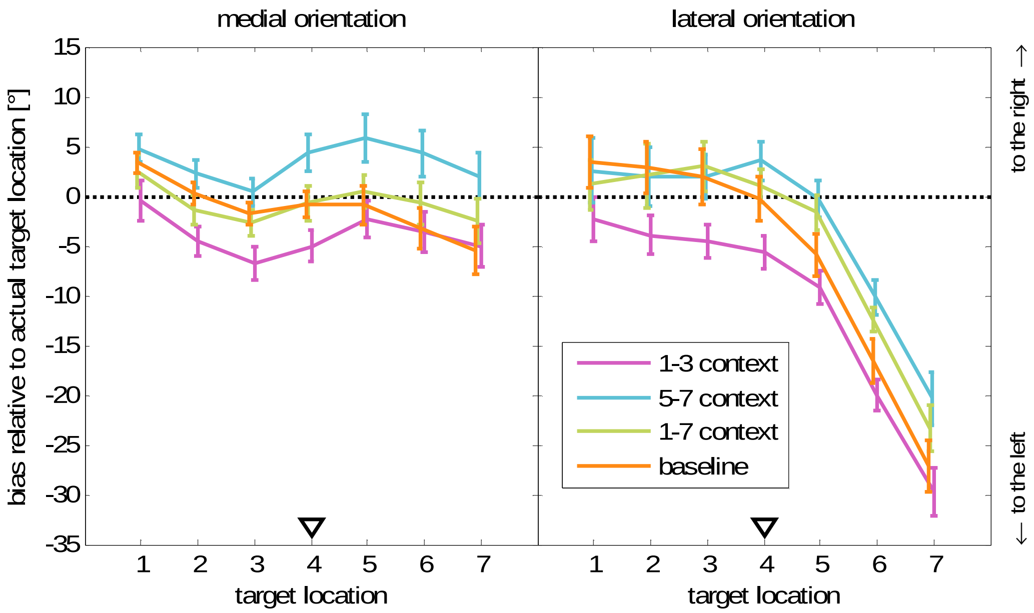

Figure 12 Bias relative to actual target location as a function of actual target location identified by speaker number. Left sub-panel denotes medial orientation (subject is facing target location #4), right panel lateral orientation (subject is facing -90° relative to target location #4).

To analyze the contextual effect, we computed the bias relative to baseline condition (Figure 13). Since the different context configurations induced similar patterns for both orientations (see ANOVA further in this section), we averaged the data across the two orientations (right panel of Figure 13).

Contextual bias was induced mainly in subregion from which the context was presented (1-3 context induced bias at target locations #1-3, 5-7 context at target locations #5-7, 1-7 context at locations to both sides of the distractor). The direction of the bias at on-context side was away from the distractor (i.e., towards the side with distractor trials) and its magnitude was larger when context was presented only on one side of the distractor compared to when context was on both sides of the distractor. Contextual bias induced on one side of the distractor also generalized to middle location #4. With increasing distance of the target location relative to on-context locations, the contextual bias decreased to negligible values. Importantly, even though generalization of the bias to off-context locations was very small, the bias had the same, not opposite, direction as at on-context locations (i.e., towards the side with the context), and this was valid not only for frontal but also for lateral orientation.

These contextual bias data were subjected to repeated measures ANOVA with factors of orientation (medial, lateral), context configuration (1-3, 5-7, 1-7) and target location (1-7). ANOVA revealed significant main effect of context configuration ($F_{2,18}$=30.16, p<0.01), and significant main effect of target location ($F_{6,54}$=15.58, p<0.01). No significant interaction between context configuration and orientation was found, suggesting that different context configurations induce similar contextual bias for both orientations.

According to the observation, that the context influences mostly responses on spatially coincident targets, we restructured the responses into three groups: ON-context, OFF-context, and ON-context-ALL group, to specifically focus analysis on how context influenced locations from subregion from which it was, or was not, presented. The ON-context group contains responses on targets from locations at which in the same run also half-range context was presented (i.e., locations #1-3 for 1-3 context, #5-7 for 5-7 context). The OFF-context group contains responses on targets from locations at which no context was presented during half-range context run (#1-3 for 5-7 context, #5-7 for 1-3 context). The ON-context-ALL group contains responses on targets when context was presented at both sides of the distractor (#1-3&5-7 for 1-7 context). Target location #4 was excluded from this analysis. These coincidence groups were created separately for left and right side (subregion) of the distractor, and for each orientation.

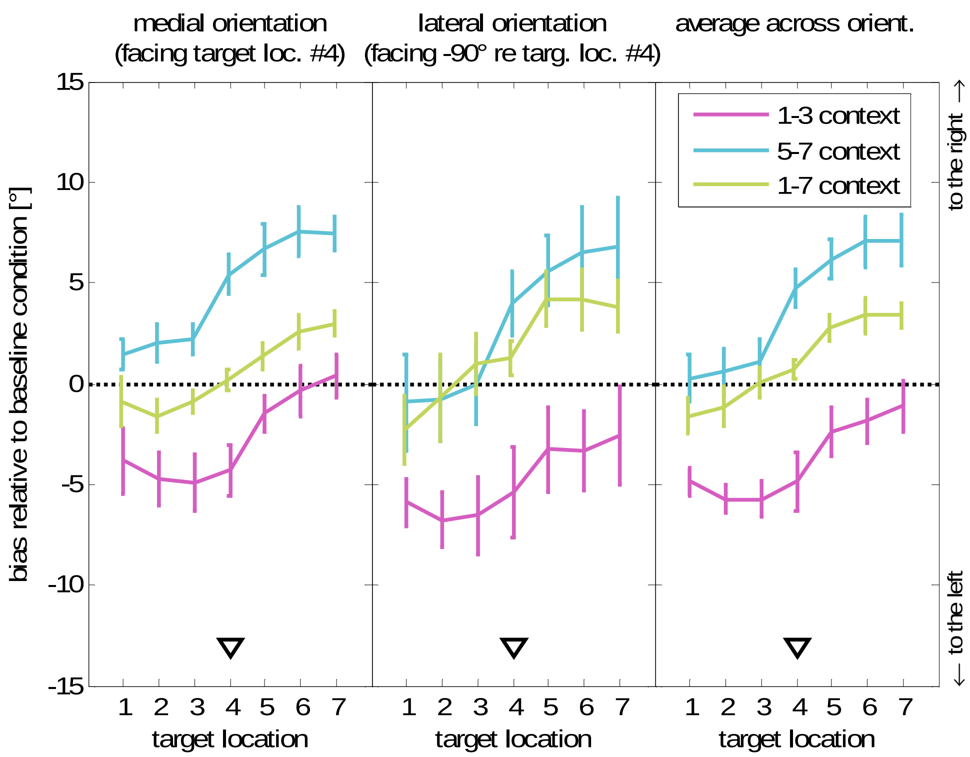

Figure 13 Contextual bias, computed as a difference between responses in context conditions and baseline condition, as a function of actual target location, for medial orientation (left-most panel), lateral orientation (central panel), and averaged across orientation (right-most panel).

Since the contextual bias was approximately the same for all locations within particular coincidence group (compare biases for all locations at the left, or at the right side of the distractor), data in each group were averaged across them. Data structured this way show the effect of the context more clearly (Figure 16). When target was presented from ON-context locations, response was biased approx. 6° away from the distractor. When context was on both sides of the distractor (ON-context-ALL), the bias was only approx. 2°, and when target was presented from OFF-context region, only negligible bias was observed.

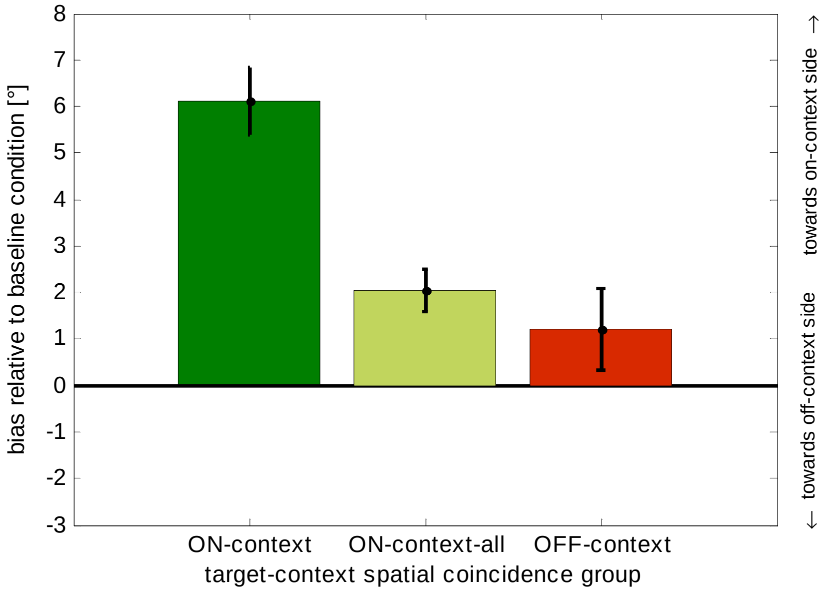

Figure 14 Contextual effect for three groups of data according to target-context spatial coincidence, averaged across subregion (left medial, right medial, left lateral, right lateral) and target locations within a subregion (#1-3). Positive bias (labeled as "towards on-context side") for ON-context-all condition represents bias away from the distractor.

Data were averaged across azimuth within a subregion and were subjected to three-way ANOVA with factors of orientation (medial, lateral), subregion (left, right), and target-context coincidence (ON-context, OFF-context, ON-context-ALL), which revealed significant main effect of the target-context coincidence ($F_{2,18}$=14.64, $p<0.01$) and significant main effect of subregion ($F_{1,9}$=12.82, $p<0.01$). Main effect of subregion indicates that the contextual bias is generally larger at one side of the distractor compared to the other. The reason for this is not clear. However, the difference is less than 2° (not shown) and hence, we will not analyze it further. On the other hand, no effect of orientation was observed, suggesting that the magnitude of the observed contextual bias is similar for both orientations. Pairwise comparisons between coincidence groups found that ON-context group significantly differs from OFF-context, and ON-contex-all group.

3.3.3 Summary and discussion

In hypothesis H2a we predicted that context presented on one side of the distractor will shift all locations in the same direction, for both orientations of speaker array relative to subject. Context presented on one side of the distractor induced contextual bias in direction away from distractor. This bias was induced mainly at on-context locations but it generalized also to neighboring locations, such that contextual bias had the same direction as at on-context side (towards the side with the distractor targets). This was observed not only for medial but also for lateral orientation, supporting our hypothesis H2a.

Another expectation about the pattern of contextual bias in Cartesian representation was that no contextual bias will be observed when context is placed on both sides of the distractor, because biases from opposite sides would cancel out, and this was expected for both frontal and lateral orientation (hypothesis H2b). This seems not consistent with results, because some bias, even though smaller than for half-range context conditions, was observed also for whole-range context condition. However, if we consider that the contextual effect did not generalize to all locations, only to closer ones, biases induced by context from opposite sides would be expected to only suppress, instead of cancelling out each other. This is consistent with results, again supporting hypothesis H2b. Another reason for lower biases might be that for whole range context, the distractor targets were presented at each distractor-target location less frequently than in half-range context (because equal number of distractor trials was divided into 6 locations, instead of 3, as in half-range context). This indirectly shows that contextual bias might depend on frequency of presentation of distractor trials, as we already reported in another study [94].

Hypothesis H2c predicted that the contextual effect will be larger for lateral than for frontal orientation. Even though subjects' responses were more accurate (relative to actual target locations) when the tested region of space was at front compared to when it was at the side, the contextual effect did not significantly differ among the two orientations, which is not consistent with hypothesis H2c. This suggests that the effect operates on such representation in which space is represented uniformly across different locations or simply that the contextual effect is based on other mechanism than the one assumed in hypothesis.

Altogether, results indicate that contextual effect does not operate on earlier stages of spatial auditory processing, at the level on which binaural localization cues ITD and ILD are processed, but on a later stage of processing, where space is represented cartesially.

3.4 Follow-up analysis: context and accuracy of responses

Results from the two experiments indicated possible underlying neural representation of the effect, but they did not explain why the effect occurs, since its relation to the listener's localization strategy stemming from an effort to separate the distractor from the target was not supported. In this section, we will consider another possible explanation of the effect.

This explanation is based on the temporal profile of responses within a run (i.e., how responses evolved during a run; see Figure 15). It shows that responses in baseline condition, which were expected to be relatively stable for particular target location, actually in some conditions (especially lateral orientation of the listener relative to the speaker array, shown in the figure) drifted during the time course of the run towards subject's straight ahead. On the other hand, responses in context conditions, even though initially biased due to context (in the 3rd subrun, in which the distractor trials were first presented) remained approximately constant, while the context was provided (until 10th subrun). Baseline drift might be caused by the fact that subjects had their eyes closed and hence they lost visual feedback, or "anchors" which helped to define the boundaries of the tested spatial region. In distractor runs, repeated presentation of distractor from the same and a priori known location (and possibly also the repeated presentation of distractor targets) might also act as an anchor, relative to which subjects judge the location of other sounds. In other words, instead of absolute localization, in which the location of the sound is judged according to ITD and ILD values of the target sound, and which seems to undergo temporal drift, subjects might use relative localization, in which the sound is localized relative to ITD and ILD of the stable location of the distractor (and possibly also of distractor targets). Hence, after initial inducement of a bias in responses, context might help to "fixate" the spatial auditory representation.

In order to test the hypothesis that context improves mentioned aspects of localization, we focused on other measures of localization accuracy except for how responses are biased relative to actual target locations, specifically on: 1) correlation of responses with actual target locations, and 2) standard deviation of responses for particular target location.

We hypothesize that:

Hypothesis H3a: Context will improve correlation of responses with actual target locations.

Hypothesis H3b: Context will decrease standard deviation in responses for a particular target location.

Data from Experiment 2 were used in this analysis. Data were subjected to repeated measures ANOVA. Box-Geisser-Greenhouse correction was used, which adjusted degrees of freedom. We report uncorrected degrees of freedom for F-values and corrected p-values.

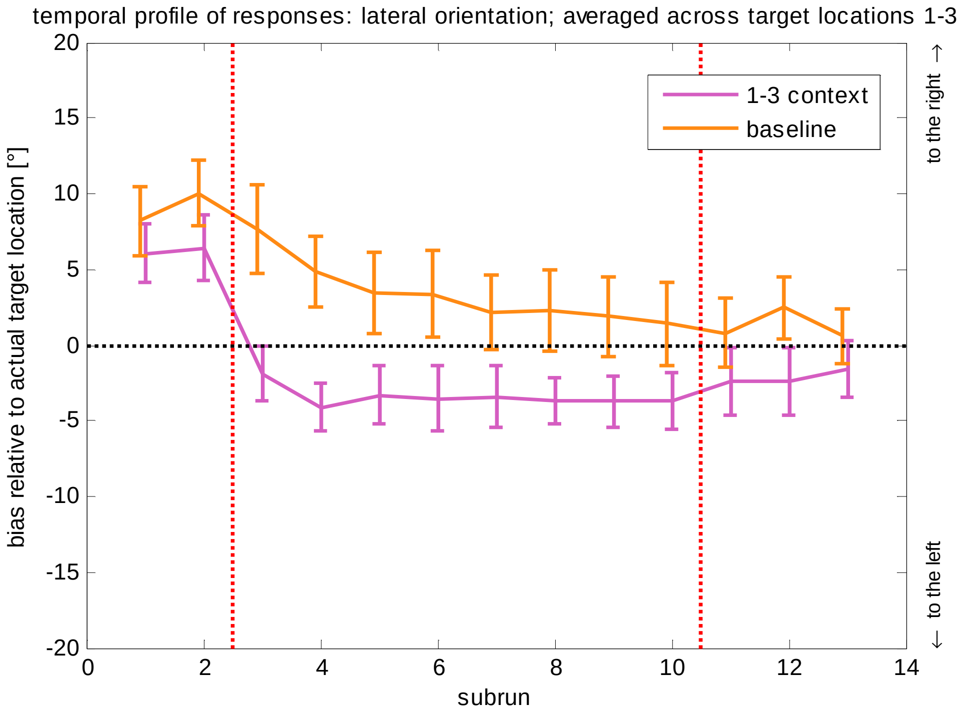

Figure 15 Temporal profile of responses (bias relative to actual target location as a function of subrun number) for lateral orientation, target locations #1-3 (averaged across target locations). Red dotted line indicate beginning and the end of the adaptation part of the run.

3.4.1 Correlation of responses with actual target locations

Pearson product-moment correlation coefficients (CCs) between actual target locations and subject's responses on no-distractor trials from subruns 4:10 (same as in previous analysis of biases) were computed separately for each run.

Runs with very low CC (below 0.3) were excluded (only two runs altogether).

Before performing analyses, we transformed the values of correlation coefficients by Fisher Z-transform (Equation (1), in which *ln* is natural logarithm function, *artanh* is inverse hyperbolic tangent function, and *r* is sample correlation coefficient). The reason for applying the transformation is that the sampling distribution of CCs is not normal, i.e., as values approach values 1 or -1, they become skewed and averaging and comparisons of different values of CCs could lead to misinterpretations. Fisher Z-transform changes sampling distribution to normal and enables further statistical processing of correlation coefficients.

$$z = \frac{1}{2} ln\left(\frac{1+r}{1-r}\right) = arctanh(r) \qquad (1)$$

In general, correlations between actual target locations and subjects' responses were high when subject was oriented towards the central speaker medially (around 0.96) but were lower when he/she was oriented laterally (around 0.8; Figure 16). In analysis of bias for lateral orientation, it was revealed that subjects had problems with localizing targets presented behind interaural axis – their responses were skewed towards the center of the speaker array (see subchapter 3.3 Experiment 2, Figure 12), what is the reason for lower correlation coefficients for lateral orientation.

Even though CCs differ between medial and lateral orientation, the difference in CC between baseline and other condition within the same orientation are similar for both orientations (compare orange line to other lines in medial and in lateral orientation in Figure 16). Two-way ANOVA with factors of orientation (frontal, lateral) and context (1-3 context, 5-7 context, 1-7 context, baseline) revealed significant main effect of orientation ($F_{1,9}$=341.74, $p<0.01$) and main effect of context ($F_{3,27}$=5.52, $p<0.05$). Pairwise comparisons showed that baseline significantly differs from each condition with context.

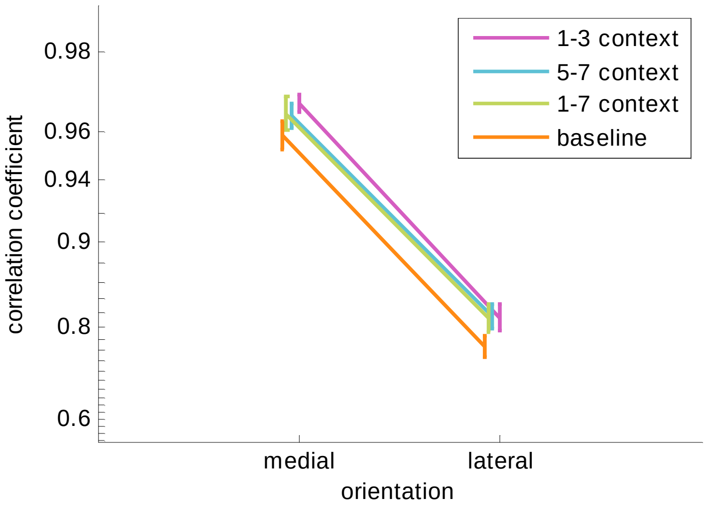

Figure 16 Correlation coefficient as a function of subject's orientation relative to the speaker array, for different context conditions. Data were transformed by Fisher Z-transform, averaged across repetitions and then plotted. The values on y-axis were transformed back from Fisher-transformed values to values of correlation coefficient, allowing easier interpretation of results.

Contextual effect is plotted in Figure 17. Since there was no difference in effect of the context between the two orientations, data were averaged across orientation. Context improved correlation coefficients in comparison to baseline, but no significant effect of context configuration was found. Hence, context improved correlation of responses with actual target locations, not depending on where the inducing distractor-targets were located.

Correlation coefficients computed so far considered whole target locations range and did not allow us to compare whether the context affects only subregion in which it is presented or also other locations. Thus, we performed subregion analysis (analogous to the one applied on contextual bias already discussed before), in which we divided the data from distractor runs into ON-context, OFF-context, and ON-context-ALL groups, and computed correlation coefficients only from target locations within specific subregion (left or right, speaker 4 was excluded).

Figure 18 shows CCs computed according to the subregion analysis. CCs are in general smaller than in previous analysis in which all target locations were included for computation of the CC (compare CCs in Figure 18 vs Figure 16). The decrease in CC is given by a property of CC, according to which decreasing the range of one of the variables leads to decrease in the correlation coefficient [65].

Similarly to previous analysis, CCs are better for medial orientation than for lateral orientation (compare left vs right panel in Figure 18) and are very low especially for target locations behind interaural axis (only approx. 0.1), as already discussed previously.

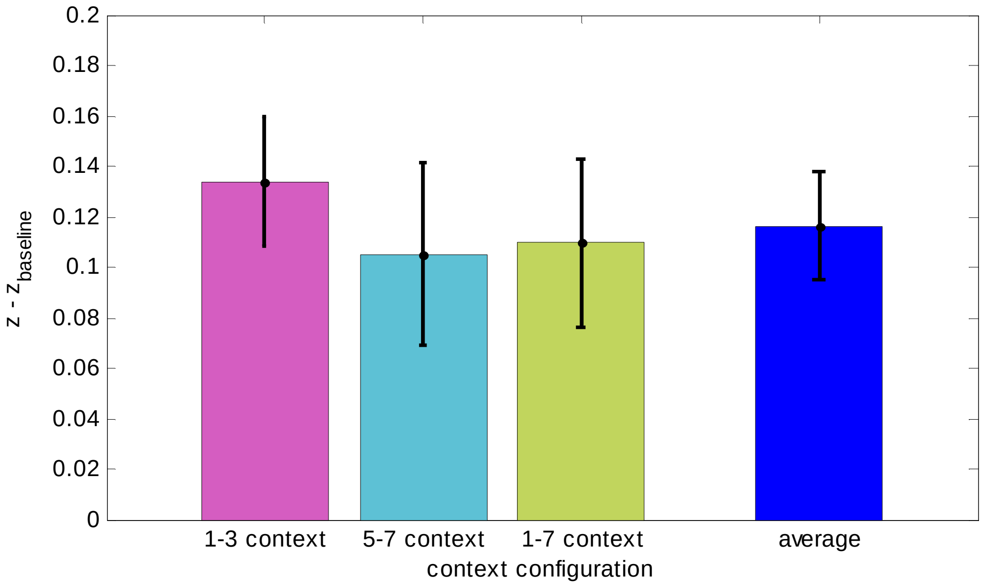

Figure 17 Contextual effect computed as a difference in transformed correlation coefficients for different context configurations and a baseline condition, averaged across orientation. Right-most bar shows average across the three left bars.

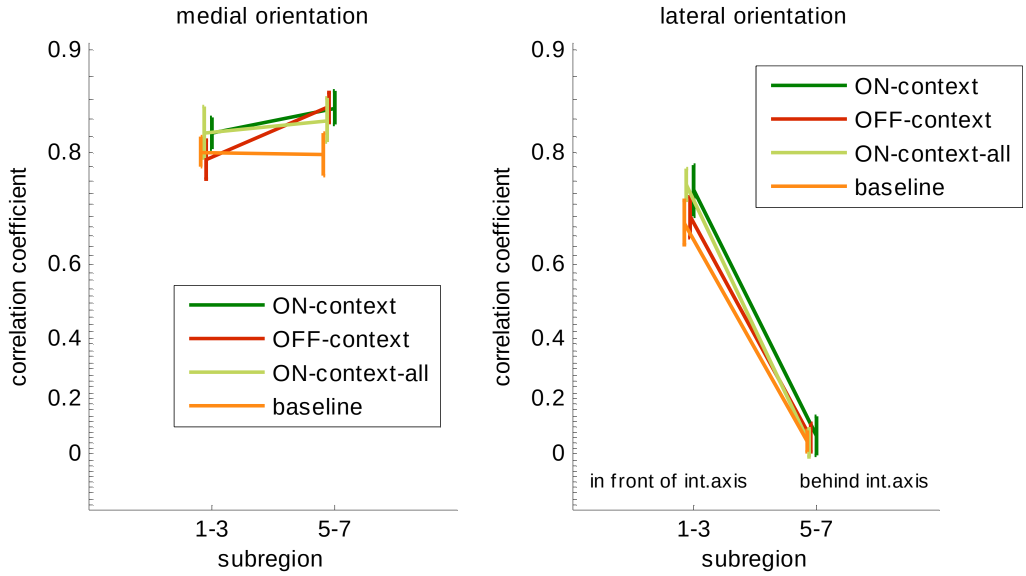

Figure 18 Correlation coefficient for medial (left panel) and lateral (right panel) orientation, for different subregions.

Since for locations behind interaural axis subjects behaved differently than in other subregions and their responses did not correlate with actual target locations, data behind interaural axis were excluded from analysis. Factors subregion and orientation were restructured into new factor subregion with three levels: 1-3 medial, 5-7 medial and 1-3 lateral.

Remaining data were subjected to two-way ANOVA with factors of subregion (1-3 medial, 5-7 medial, 1-3 lateral) and context group (ON-context, OFF-context, ON-context-all, baseline). Significant main effect of subregion was found ($F_{2,18}$=9.72, p<0.01), which only reflects the fact that CCs are worse for lateral data. Even though not reaching significance when Box-Geisser-Greenhouse corrections were applied, only without them, main effect of context group was also observed, with ON-context and ON-context-all groups significantly different from baseline. Figure 19 shows the contextual effect for different context groups averaged across subregion. The context increased correlation coefficients at ON-context, and ON-context-all groups, while almost no effect is observed for OFF-context data.

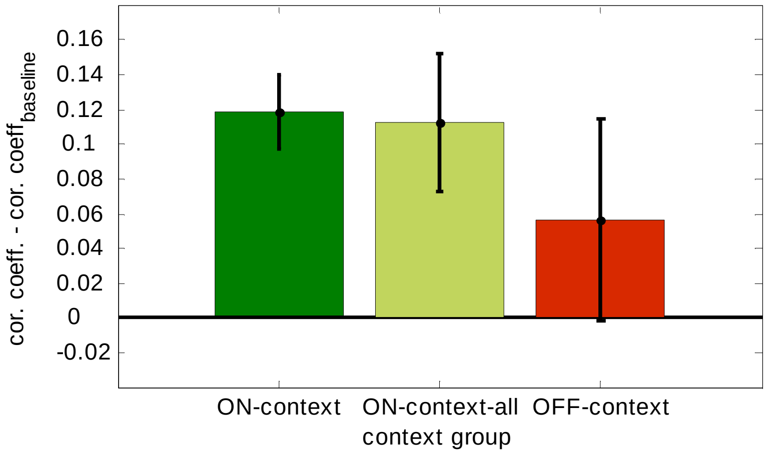

Figure 19 Contextual effect as a difference in CCs between conditions with context and baseline condition for different context groups, averaged across subregions 1-3 medial, 5-7 medial and 1-3 lateral.

3.4.2 Standard deviations of responses on particular target location

Standard deviations (SDs) were computed from no-distractor responses from subruns 4:10 (same as biases and correlation coefficients), separately for each run and target location.

Figure 20 shows SDs as a function of target locations for both orientations and all context conditions. SDs were in general lower when subject was oriented medially towards central speaker (approx. 5-6°) than when he/she was oriented laterally (approx. 7-10°, compare left and right panel in Figure 20), what is probably a consequence of better spatial resolution at frontal locations compared to lateral locations (see also chapter 2.1.7 Accuracy of sound localization). Moreover, the overall spatial pattern of the lateral data is slightly V-shaped (when we don't consider left-most target location; note that SDs increase from center to the side of the array), what might be explained by increased front-back confusions (increase of SDs with increasing distance of the target relative to interaural axis).

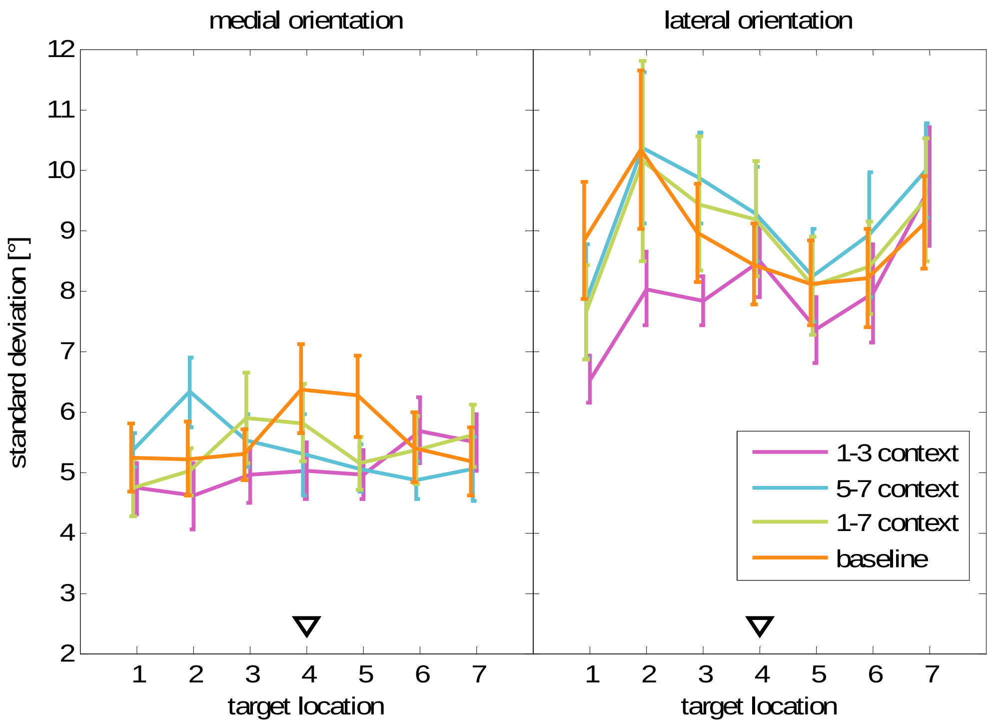

Figure 20 Standard deviations of responses as a function of target location for medial orientation (left panel) and lateral orientation (right panel). Location of the distractor is marked by triangle above x axis.

Three-way ANOVA with factors of orientation (medial, lateral), target location (1-7) and context (1-3 context, 5-7 context, 1-7 context, baseline) found significant main effect of orientation ($F_{1,9}=34.60$, $p<0.01$) (due to higher SDs for lateral orientation), signif. main effect of target location ($F_{6,54}=5.33$, $p<0.01$) (due to v-shaped spatial pattern of lateral data) and signif. main effect of context ($F_{3,27}=4.41$, $p<0.05$).

Signif. main effect of context suggests that context affected also standard deviations of responses. The contextual effect is plotted on Figure 21. When we don't consider data behind interaural axis, which were problematic also in previous analyses of biases and correlation coefficients, the contextual tends to lower SDs in the subregion from which the context was presented, while it had almost no effect on the other subregion (pink line is lower on the left side of the distractor than on the ride side, and blue line vice versa). When context was presented on both sides of the distractor, the contextual effect tends to be smaller (yellow line is closer to 0).

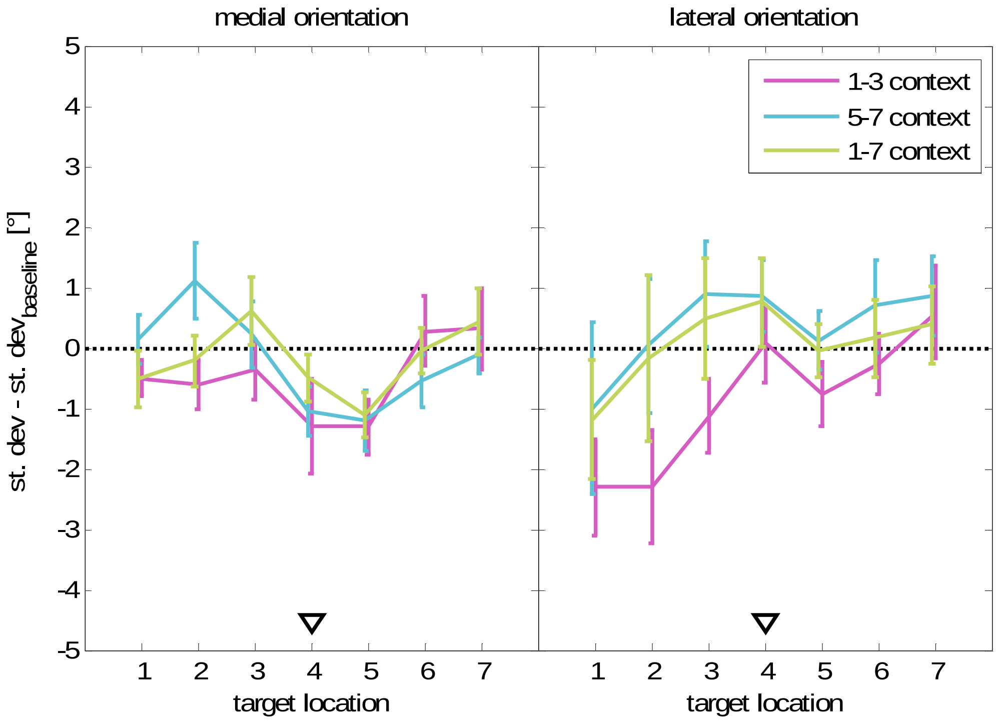

Figure 21 Contextual effect computed as a difference in SDs of no-distractor responses from distractor runs vs SDs of responses in baseline, plotted as a function of target location, for medial orientation (panel A) and lateral orientation (panel B). Location of the distractor is marked by triangle above x axis.

These observations can be better examined by subregion analysis, with data restructured into groups according to target-context spatial coincidence within a run (in the same way as in analysis of bias or correlation coefficients). Data behind interaural axis were excluded. Data in this form were subjected to three-way ANOVA with factors of subregion (1-3 medial, 5-7 medial, 1-3 lateral), target-context spatial coincidence (ON-c., OFF-c., ON-c.-ALL, baseline) and target location relative to distractor (1,2,3).

Significant main effect of subregion ($F_{2,18}$=28.51, p<0.01), signif. main effect of target-context spatial coincidence ($F_{3,27}$=5.88, p<0.05) and signif. main effect of target location ($F_{2,18}$=4.63, p<0.05) (which stem from already discussed observations) was found. Even though pairwise comparisons did not reveal significant difference between baseline versus any of the remaining levels of factor target-context spatial coincidence, data suggest that ON-context responses tend to have lower SDs relative to baseline, while responses on OFF-context and ON-context-ALL tend to be similar to baseline (Figure 22; with data behind interaural aixs also shown even though not included in analyses), supporting the idea that context affects responses only in subregion in which it was presented.

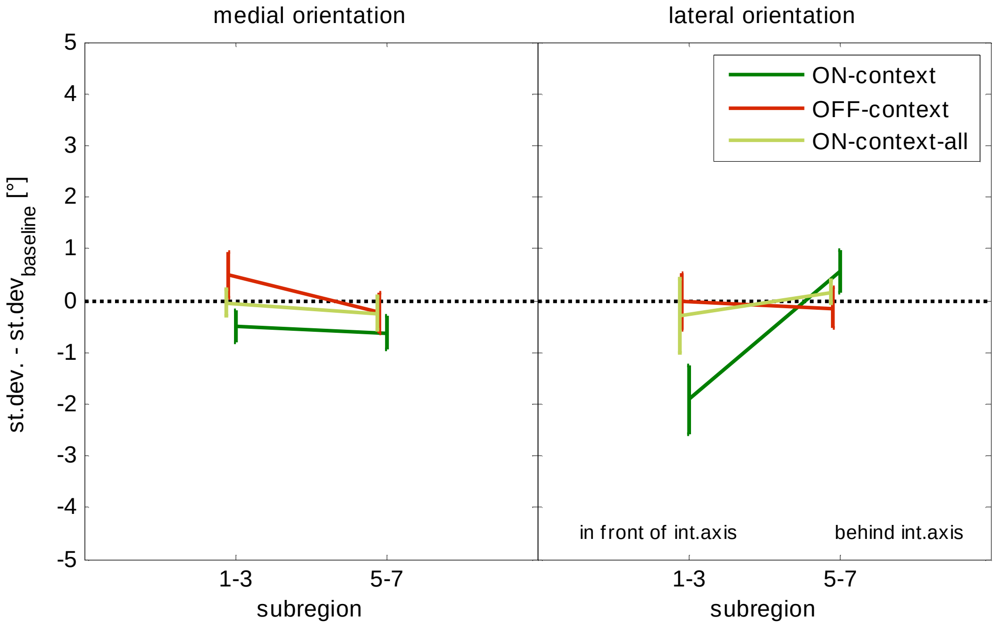

Figure 22 Contextual effect as a difference between SDs of no-distractor trials vs SDs of baseline, for three subregions, averaged across target locations within the same subregion.

Given that standard deviation depends on number of samples used, and since number of samples was not the same for each condition (7 for distractor runs and 28 for baseline, see chapter 3.3.1 Methods), our comparisons of SDs may be incorrect. In order to statistically compare standard deviations properly we restricted the number of samples in baseline to match the number of samples in distractor runs. Thus, both types of runs were balanced and had 7 samples. To preserve possible temporal effects during the run, samples were chosen uniformly throughout the run (specifically, 28 samples were divided into 7 bins, while keeping the temporal order of the samples, and first sample of each bin was chosen).

ANOVAs performed on balanced data revealed the same effects as ANOVAs on non-balanced data, except that in the first ANOVA, in which different context configurations were tested, the effect of the context was significant only when Box-Geisser-Greenhouse corrections were omitted ($F_{3,27}=3.45$, $p<0.05$). Moreover, in the second ANOVA, in which an effect of target-context spatial coincidence was tested, in addition to main effects observed also in non-balanced ANOVA, a significant interaction between factors subregion and target location was also found ($F_{4,36}=3.45$, $p<0.05$)

3.4.3 Summary

In hypothesis H3a we predicted that context will improve correlation of responses with actual target locations. The results were consistent with the hypothesis - the context with each of the considered spatial configurations improved the correlation. Another positive effect of the context was that it improved (i.e., decreased) also standard deviation of responses on target from specific location (supporting hypothesis H3b). Effect of the context was only small, but significant. Moreover, in both of these measures, the context tended to affect only locations at which it was presented.

These results are consistent with the explanation that listener use the contextual stimuli and as an anchors in localization leading to more stable responses and more correlated mapping between responses and actual target locations. Since the improvement was observed

3.5 Discussion of all experimental results

Both experiments confirmed that the context of distractor trials affects responses on interleaved no-distractor trials. The context induced bias of a few degrees away from the distractor location. This contextual bias was induced mainly at locations between the distractor and distractor-targets (including also their locations), as if the presentation of the distractor and subsequently following target stretched the space between the two stimuli away from the distractor.

However, several inconsistencies were observed between the two experiments. For example, context close to the distractor induced biases of different magnitudes between the two experiments (approx. 2° in Experiment 1 and 6° in Experiment 2). This difference might be caused by slightly different setup between the experiments – in Experiment 1, possible target locations were situated only on one side of the distractor, while in Experiment 2 they were situated at both sides of the distractor. Knowledge about possible target locations (or, from a bottom-up view, activation of the neural representation caused by presenting no-distractor targets from these locations) might interact with the contextual effect. Another difference was in the effect of the distractor location. In Experiment 2, frontal distractor induced effect of approx. the same magnitude as the effect induced by lateral distractor, but in Experiment 1 the frontal distractor induced larger biases. The reason for the difference might also stem from where the non-context stimuli are located.

When considering bias as the performance measure, the effect of context was mostly negative, shifting responses away from the actual target locations (depending on accuracy of responses in baseline condition and context configuration). However, when considering other performance measures the effect of context was positive, resulting in increased correlation between the actual locations and response locations and in decreased response variance. This indicates that the presence of context resulted in a more stable mapping between the target and response locations. However, due to a persisting bias relative to actual target location, context cannot be considered as improving localization in general. Additional analysis of the responses in distractor trials could reveal more about the cause of the contextual effect.

4 Model of contextual bias

This chapter describes the computational model of the contextual bias we designed in order to explain the results from the two experiments. The model is based on a place code and assumes that the context stimuli (i.e., distractor-targets) induce local biases in the neural representation of auditory space. We will test four variants of the model (described later in the text), differing in the assumptions about the spatial characteristics of the neural representation and interactions between its units.

4.1 Introduction

4.1.1 Data chosen for modeling

The model focuses only on spatial aspects of the contextual effect and does not cover other aspects of localization. Instead of modeling each particular response in the experiment, we focused on contextual bias averaged across the adaptation period and across subjects, for different target locations (as it was analyzed in the experiments; see Figure 23). The reason for considering this latter stage is that raw responses are subjected to other factors such as, for example, edge effect, in which responses on target locations are shifted towards the center of the speaker array (observed in Figure 12), or effect of cone of confusion, which introduces front-back errors into responses, etc. Some of these factors might be associated with specific setup or method of responding and are not directly related to the contextual effect. In order to model the pure contextual effect, we avoided these early stages.

We also did not consider distractor location (or speaker array orientation) relative to subject as a significant factor, because the two experiments differ in whether the factor was significant (possible reasons are discussed in section 3.5 Discussion of all experimental results). And since it did not influence the pattern of the contextual bias only its magnitude, we averaged the results across frontal and lateral orientation (or frontal and lateral distractor conditions; averaged data are depicted on left-most and right-most panels of Figure 23).

Since we also assumed symmetry of the contextual bias relative to the distractor location, we restructured the data such that symmetric conditions within one experiment were collapsed and averaged. Specifically, for Experiment 2 we collapsed the data across the context conditions „1-3 context“ and „5-7 context“ and across left and right subregion for „1-7 context“ condition (i.e., in left panel of Figure 23, to get the half-range context bias, we flipped the pink line across x-axis and vertical axis crossing target location 4, and averaged it with blue line, and to get whole-range context bias we did the same for target locations 1-3 of the yellow line and averaged it with bias at target locations 5-7). Resulting biases are shown on Figure 24, with yellow line showing resulting data for whole-range context and violet line for half–range context. The same restructuring was performed also on data in D45 condition from Experiment 1. D0&D90 averaged data remain in the same form asi in Figure 23. Data in this form will be subjected to modeling.

The three sets of the data as are depicted on separate panels of Figure 23 but with mentioned restructuring of data for the two left-most panels will be modeled separately.

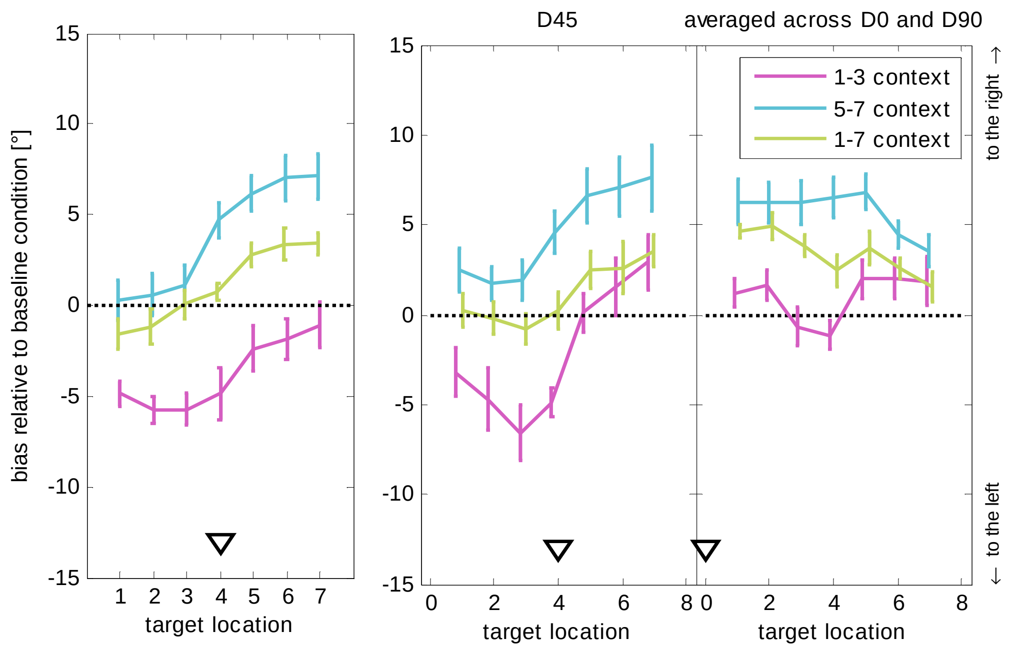

Figure 23 Contextual bias data chosen for the model. Left panel shows contextual bias from Experiment 2, averaged across orientation and two right panels show contextual bias from Experiment 1, for D45 condition (left sub-panel) or averaged across D0 and D90 conditions (right sub-panel). For more detailed description, see Experimental part. Distractor location is marked by a triangle above x axis.

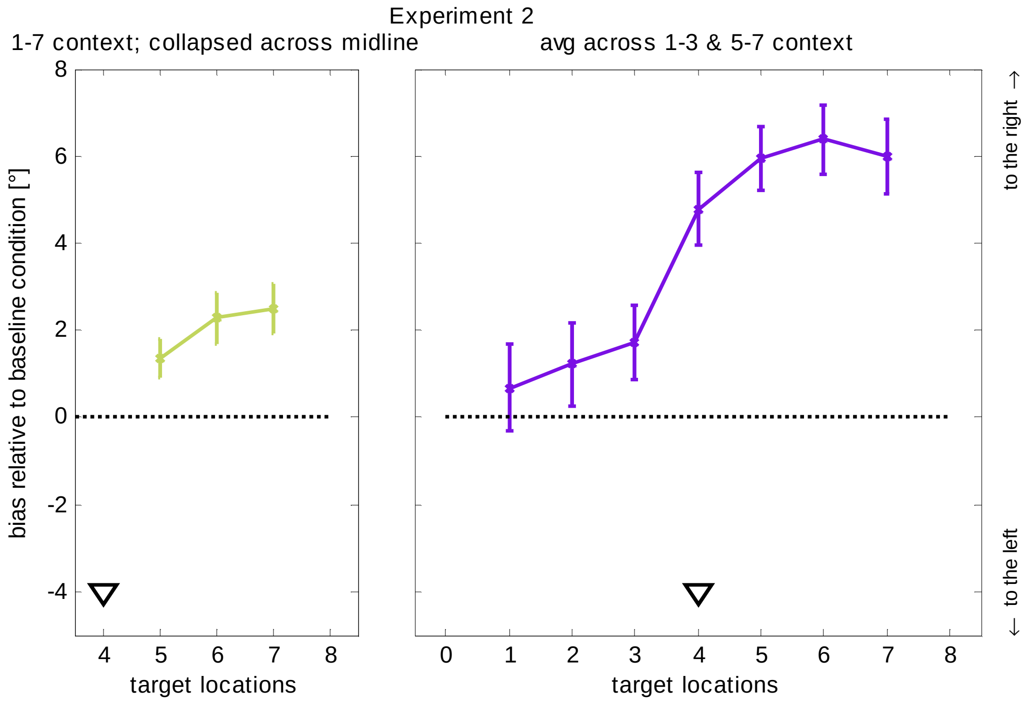

Figure 24 Contextual bias data (only Experiment 2 shown) in a form which will be subjected to the model. Yellow line combines 1-7 context data from symmetric locations relative to the distractor location and violet line combines data from 1-3 context and 5-7 context conditions (depicted as if the context was on locations 5-7). Distractor location is marked by a triangle above x axis. Directions of the biases are labeled according to how the context configuration is depicted on a figure.

Factors found to influence the contextual bias and considered in the model are:

- distractor location relative to tested spatial region (determines the direction of the bias for each location)
- context configuration (affects at which of the considered locations the bias will be induced),
- percentage of distractor trials within adaptation part of the run (affects the magnitude of the contextual bias – higher percentage of distractor trials leads to larger contextual biases, as we observed in different study of contextual effect [94]).

The latter two factors can be merged into one: spatial distribution of the context, which signifies the proportion of distractor-targets presented from each target location.

4.1.2 Basic structure and mechanism of the model

In general, there are two types of models of how the auditory space is represented in the brain, supported by neurophysiologic observations: place code models and hemifield code models (see chapter 2.3.3 Models of plasticity in sound localization), differing in whether the location is coded by locus of activity in topographically organized array of narrowly-tuned neurons or whether it is coded by comparison of activities of two broadly tuned (left-tuned and right-tuned) groups of neurons. We assume that the contextual effect observed in our study is caused by frequent presentation of the distractor and distractor-targets associated with local neural changes (for example in sensitivities of neurons) in the spatial representation. The hemifield code representation could not lead to contextual biases of different directions within the same hemifield. Instead, all within-hemifield locations should be shifted in one direction. Since more complicated spatial patterns of the contextual bias were observed in our study, even in condition in which all the stimuli were within one hemisphere, we assumed that our model does not operate on hemifield-code representation of auditory space.

Thus, we represented the tested spatial region from the experiments by topographically organized units centered at possible target locations. However, even when operating on a place code representation of auditory space, the contextual effect might use such mechanism, which does not affect only units with receptive fields at distractor-targets locations (and adjanced locations), but also more distant units. This is supported by Experiment 1 in which biases were observed also at locations between the distractor and the distractor-targets.

Hence, we assume that the presence of the distractor-target at particular location induces bias away from distractor at this location, and other locations defined by specific neighborhood function. We tested two neighborhood functions: Gaussian or sigmoidal. Each type of neighborhood suggests different spatial mechanism on which the contextual effect operates. Gaussian neighborhood points to a place code mechanism, in which each unit influences only its local neighborhood (similar to a conceptual place-code model of adaptation described by Carlile et al. [24]), while sigmoidal neighborhood refers to a kind of two-channel mechanism in which each unit influences all units to the left or to the right relative to some reference point given by location of the distractor-target (the reference point does not have to be median plane as in hemifield code representation; similar to model proposed by Zwiers et al. [29]). Further in the text we might refer to these mechanisms as “representations”, while meaning representation of how the contextual effect affects underlying place code representation of auditory space (since hemifield code was ruled out).

Moreover, even though target locations in the experiment are distributed uniformly in space, underlying spatial neural representation does not have to be uniform. Our results from analysis of bias show that subjects had tendency to shift all responses towards the center of the response range (Figure 12). This suggests that when the range of possible target locations is restricted, representation of space at some later stage of spatial processing pathway is non-uniform. This also applied to baseline condition which was the reference for computation of the contextual effect. We assumed that by transforming linear space (vector of uniformly distributed 7 spatial units) into nonlinear space, model might give better results.

The aim of the modeling was to find a simple model which would be able to describe the data and which would consider also possible underlying representation of the effect and mechanisms it involves.

Due to the fact that a generalization of the contextual effect was found also to target locations farther away from the on-context region, we hypothetize that:

Hypothesis H4: Sigmoidal neighborhood will provide a better fit of the data than Gaussian neighborhood.

4.1.3 Detailed structure of the model

Our model is based on topographically organized units representing spatial locations. To simplify the model, we use such number of units which is equal to number of active speakers within an experiment (each unit represents target/distractor location). The model has three input parameters which are to be set according to specific condition within an experiment:

- target locations X_i, where i=1,…,N (fixed for both experiments presented here but allows examination of other location in possible future experiments)
- spatial distribution of the context C_i, where i=1,…,N (signifies the number of distractor-targets presented from each target location; such that the sum

of the numbers across all locations is scaled to the number representing percentage of distractor trials within adaptation part, i.e., fixed at 75% in current experiments)

- location of the distractor *D*

Possible values of these parameters for the two experiments presented in this thesis are listed in Table 1.

	Target locations (**X**)	Context configuration (**C**)	Location of the distractor (D)
Experiment 1	[1,2,3,4,5,6,7]	[0, 0, 0, 0, 25, 25, 25], [25, 25, 25, 0, 0, 0, 0], [12.5, 12.5, 12.5, 0, 12.5, 12.5, 12.5]	0,4,8
Experiment 2	[1,2,3,4,5,6,7]	[0,0,0,0,25,25,25], [25,25,25,0,0,0,0], [12.5, 12.5, 12.5, 0, 12.5, 12.5, 12.5]	4

Table 1 Summary of parameter values used for modeling the data in Experiment 1 and Experiment 2.

Distractor-targets at particular target location X_j induce contextual bias *b* at locations within neighborhood of X_j, in direction to the left/right according to whether the location X_j is to the left or to the right of the distractor (see equation (1)). The magnitude of the bias induced by distractor-targets at spatial unit *j* will be estimated according to number of distractor-targets at this spatial unit, C_j. The neighborhood is defined by neighborhood weighting function *w*, which can be either Gaussian (equation (2a)), or sigmoidal (equation (2b)). By summing these partial biases at spatial unit *i* from different distractor-target locations, we get the overall contextual bias for spatial unit *i* (equation (3)). The bias is scaled by factor *k* and increased/decreased by offset parameter *q*.

Equations for computation of the contextual bias, with explanation of symbols used are stated in the text below:

N .... number of spatial units

X_{i},................. target location represented by i-th spatial unit; i,=1,...,N

D................. location of the distractor

$bias_i$ .... contextual bias induced at spatial unit i; i,=1,...,N

$b_{i,j}$ .... partial contextual bias induced at spatial unit i by distractor targets at spatial unit j; i,j=1,...,N

w…................ neighborhood weighting function

C_j .... number of distractor targets presented from spatial unit j; j,=1,...,N

k .... scaling factor

q .... offset parameter

weighting functions parameters:

σ .... gaussian width parameter

a .... modifies shape and orientation of the sigmoid

s .... shift of the sigmoid's inflection point relative to specific distractor-target's location

i,j=1,...,N

$$b_{i,j} = \begin{cases} C_j w(X_i;\sigma,X_j), & for\ X_j > D \\ -C_j w(X_i;\sigma,X_j), & for\ X_j < D \end{cases} \quad (1)$$

$$\mathrm{w}(X_i;\sigma,X_j) = e^{\frac{-(x_i-x_j)^2}{2\sigma^2}} \qquad \sigma > 0 \quad (2a)$$

$$w(X_i;a,s,X_j) = \begin{cases} \frac{1}{1+e^{a\left(X_i-(X_j+s)\right)}} & for\ X_j < D \\ \frac{1}{1+e^{-a\left(X_i-(X_j-s)\right)}} & for\ X_j > D \end{cases} \quad (2b)$$

$$bias_i = k\left(\sum_{j=1}^{T} b_{i,j}\right) + q \qquad k,q \in \mathbb{R} \quad (3)$$

Tested variants of the model differ also in whether the spatial representation on which they operate is uniform or not. The spatial units in the model are represented by an array with elements stating positions of tested location in space. In uniform representation the positions are distributed with equal step. We used the simplest notation **X**=[1,2,3,4,5,6,7], while the step of 1 actually represents 11.25 degrees, according to how speakers were placed in the experimental setup. In non-uniform representation, we modified the space using sigmoid function (equation (4)), with parameters *D*, which is the x-coordinate of inflection point (in our case set according to the distractor location) and a_{space}, which controls the steepness of the sigmoid. For better comparisons of best-fit values of parameters between uniform and non-uniform space variants of the model, the transformed space is scaled to interval <1,7>.

$$X_{transf} = \frac{1}{1+e^{-a_{space}(X-D)}} \tag{4}$$

In summary, four variants of the model were tested:

- Gaussian neighborhood, uniform space
- Gaussian neighborhood, non-uniform space
- Sigmoid neighborhood, uniform space
- Sigmoid neighborhood, non-uniform space

Free parameters of the model that are fitted to the data are the parameters of the neighborhood function (σ for Gaussian, and *a* and *s* for sigmoidal), the scaling factor *k* and the offset *q*. In the model variants with non-uniform space, an additional fitted parameter is the transformation parameter a_{space}. Best fit is found by iterative least squares estimation using MATLAB function for nonlinear regression *nlinfit*. The best-fit parameter values are found for each experiment separately. Within each experiment the parameters are shared among different context configurations (i.e., the parameter values are not fitted separately for each context configuration. Instead the values are found that provide the best fit across all context configurations within a given experiment).

The procedure for finding the best-fit parameter values was performed 200 times with random initial values of parameters set from within reasonable boundaries to avoid convergence to a local minimum. For each of the simulation runs, mean squared error (MSE) was computed between best fit found and the data, and the result with the lowest MSE was chosen as the overall best-fit.

4.2 Results

4.2.1 Model with Gaussian weighting function and uniform space

In this model, the effect of distractor targets presented at a specific spatial unit *j* on other spatial units is defined by Gaussian function (equation (2a)) centered at the location of the spatial unit *j*. An example of partial contextual biases induced with the use of this function is shown on Figure 25.

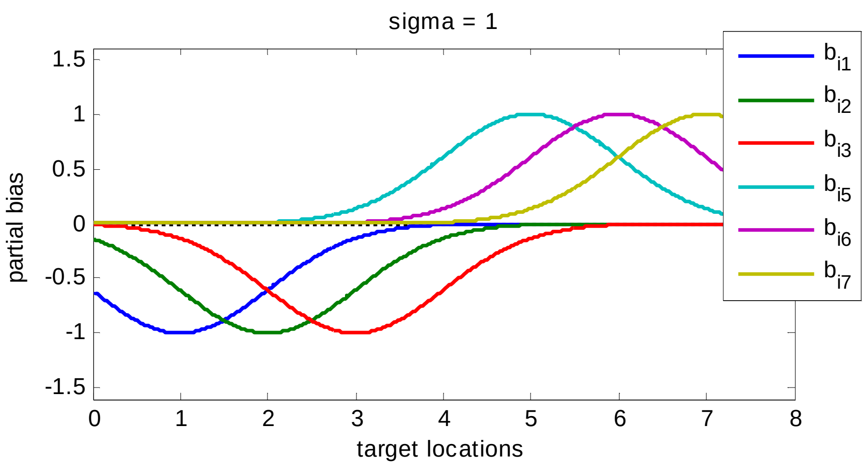

Figure 25 Example of partial contextual biases induced by distractor-targets at locations #1,2,3,5,6,7 (i.e., for 1-7 context condition). Effect of a particular distractor-target spatial unit *j* on other spatial unit is defined by a Gaussian function centered at location defined by *j*, with width defined by the parameter σ. The magnitude of the partial biases is defined by multiplying the Gaussian by input parameter C_j. In this simulation, the distractor is at location #4, therefore effect of distractor-targets #1-3 induce a leftward (negative) bias while the distractor-targets #5-7 induce a rightward (positive) bias.

First, a simpler version of the model was used, without the parameter *q*. The fitted parameters were the width of the Gaussian σ and the scaling factor *k*. Results are shown in Figure 26.

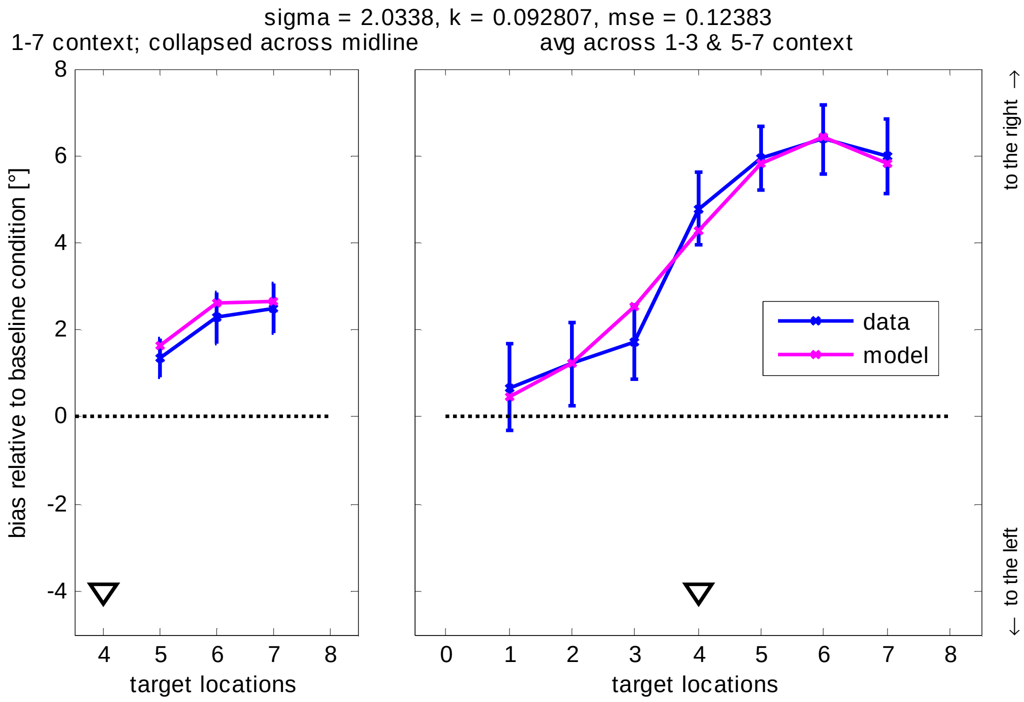

Figure 26 Comparison of the data of Exp 2 to the predictions of the Gaussian-neighborhood uniform-space model with fitted parameters σ and k. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse". In both panels data are depicted in such way that context is to the right side of the distractor.

Overall, the match between the data and the model predictions is good. The model is able to fit the „1-7 context" data well (left panel of Figure 26). It has a slight problem to fit the steep slope of the half-range context data curve between OFF-context to ON-context subregion properly (right panel of Figure 26), but large errorbars in the data suggest that the steeper slope of the data might be only a random fluctuation.

Figure 27 shows the best fit when the offset parameter q was added. Adding the offset parameter provided a further improvement to the fit (mse=0.107 vs. 0.124, Figure 27 vs. Figure 26).

The best-fit value of parameter σ was quite large, such that the neighborhood function was covering several tested target locations and within the examined spatial region almost resembled a sigmoidal neighborhood (Figure 28).

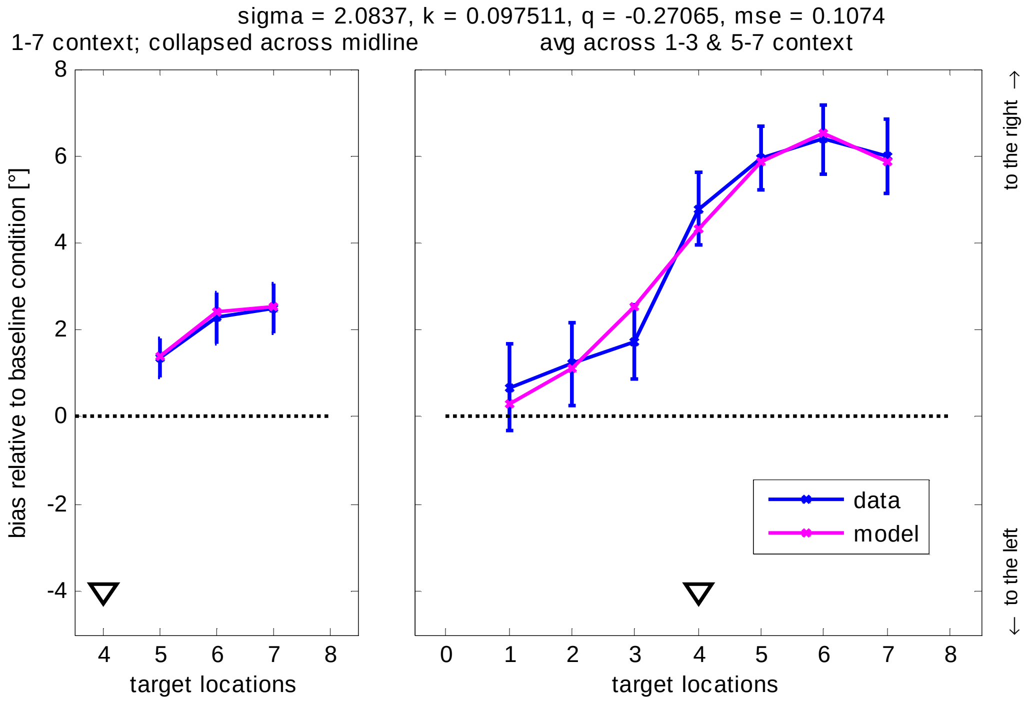

Figure 27 Comparison of the data of Exp 2 to the predictions of the Gaussian-neighborhood uniform-space model with fitted parameters *σ*, *k and q*. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse". In both panels data are depicted in such way that context is to the right side of the distractor.

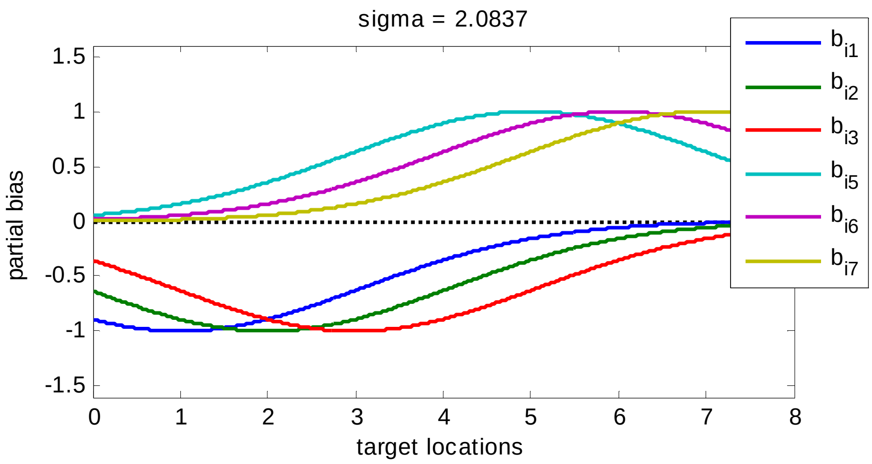

Figure 28 Partial contextual biases induced by distractor-targets at locations #1,2,3,5,6,7 (i.e., for 1-7 context condition). Effect of particular spatial unit *j* on other spatial unit is weighted by sigmoidal weighting function shifted by *s* relative to location defined by spatial unit *j* with its shape affected by parameter *a*. The partial contextual biases are in the figure scaled to magnitude of 1.

Figure 29 shows the Gaussian-neighborhood uniform-space model fitted to the data from Experiment 1. The match between the model and the data is much worse than for Exp. 2. This is given by how the magnitude of the contextual biases is computed in the model. This magnitude only depends on the spatial distribution of the distractor-targets relative to a given location. From this point of view, the 1-3 context configuration and the 5-7 context configuration are symmetrical and thus the computed biases for these locations are forced to be symmetrical (compare the pink lines in the left-hand and the right-hand panels of Fig. 29), even though in the real data they are not.

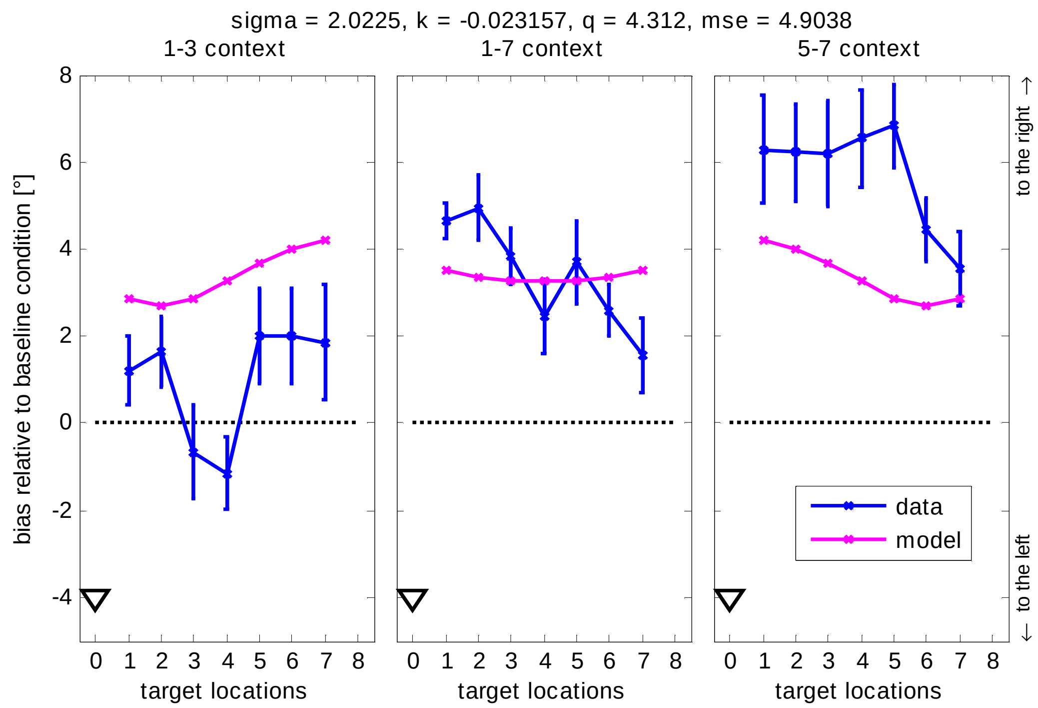

Figure 29 Comparison of the data of Exp 1 to the predictions of the Gaussian-neighborhood uniform-space model with fitted parameters *σ*, *k and q*. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse".

4.2.2 Model with Gaussian weighting function and non-uniform space

One way of modifying the model to improve its ability to describe data from Exp. 1 is to assume that the neighborhood functions are not left-right symmetrical but that locations towards the distractor location are affected differently than locations towards opposite side of the space. In addition, the shape of the neighborhood function might depend on the distance of the distractor-target location which generates it, from the distractor. In order to achieve this asymmetry we transformed the space upon which the neighborhood functions are generated.

Such a transformation of space is examined here, using the sigmoid function (equation (4)). A Gaussian weighting function from the previous version was also used in this variant of the model. The parameter of spatial transformation a_{space} was fitted by the model in addition to the parameters fitted previously (width of the Gaussian σ, scaling factor k, and offset q.) Figure 30 shows the model performance for data from Exp 2. Results show that non-linear transformation of space improved fit (mse = 0.052 in Figure 30 vs. 0.107 in Figure 27). Figure 31 shows extent to which locations were transformed.

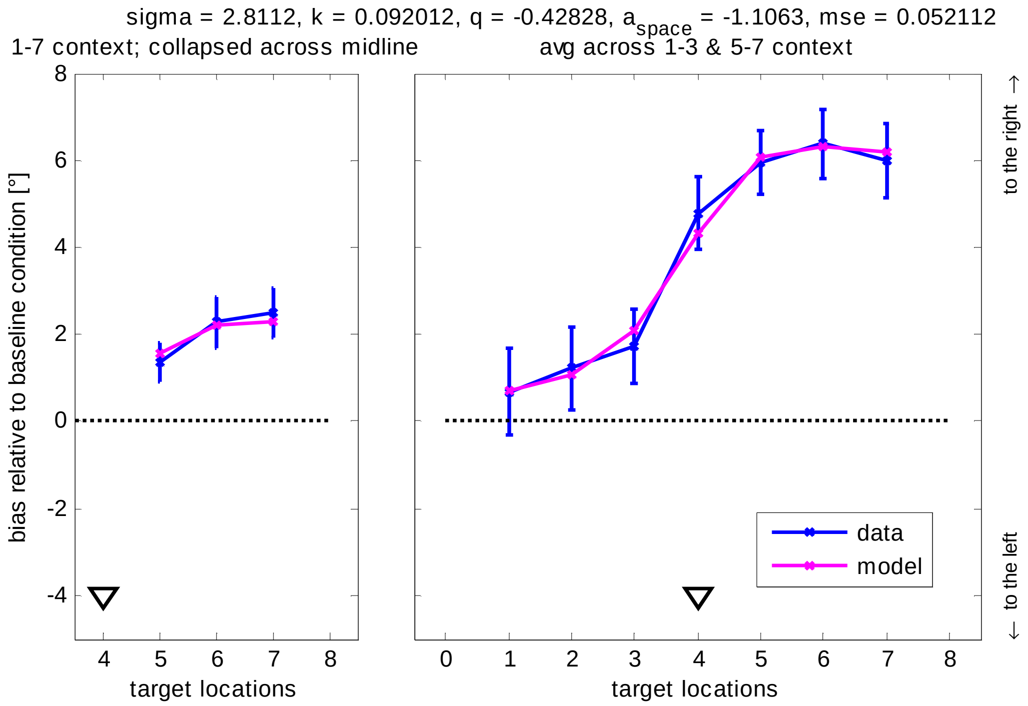

Figure 30 Comparison of the data of Exp 2 to the predictions of the Gaussian-neighborhood non-uniform-space model with fitted parameters σ, k, q and a_{space}. Best-fit model parameters are stated at the top of the figure, together with mean squared error “mse”. In both panels data are depicted in such way that context is to the right side of the distractor.

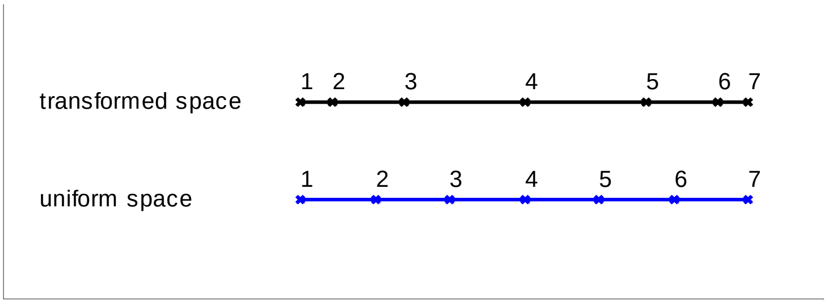

Figure 31 Transformation of space with best-fit value of parameter a_{space} = -1.1063 and rescaled to <1,7> compared to uniform space.

This variant of the model was not able to fit data from Experiment2 (Figure 32). In the process of fitting the parameter values, the model tended to increase the steepness of the space modifying sigmoid such that resulting transformations of space were computationally problematic to handle and also not reasonable (see Figure 33).

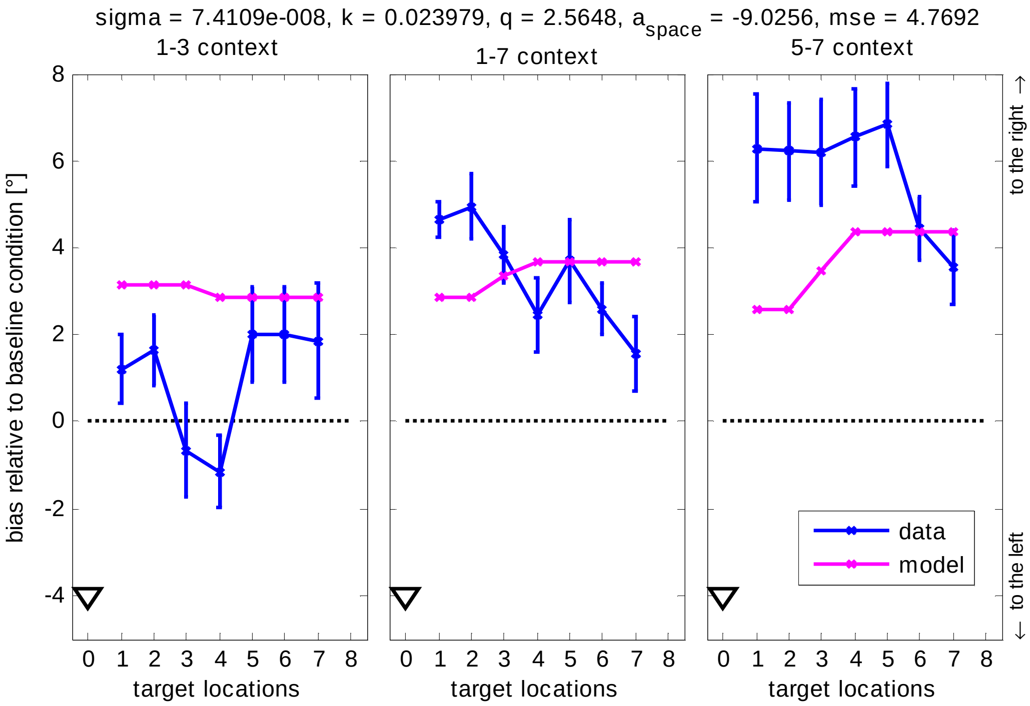

Figure 32 Comparison of the data of Exp 1 to the predictions of the Gaussian-neighborhood non-uniform-space model with fitted parameters *σ, k, q and* a_{space}. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse". In both panels data are depicted in such way that context is to the right side of the distractor.

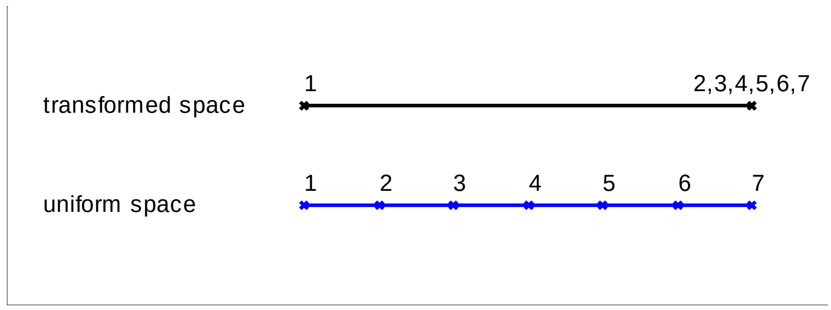

Figure 33 Transformation of space with best-fit value of parameter a_{space} = -9.0256 and rescaled to <1,7> compared to uniform space.

4.2.3 Model with sigmoidal weighting function and uniform space

In this model, the effect of distractor-targets from specific spatial unit *j* on other spatial units is defined by sigmoidal weighting function (equation (2b)) with its inflexion point shifted relative to the location defined by spatial unit *j* by *s*. An example of partial contextual biases induced with use of this function is shown on Figure 34.

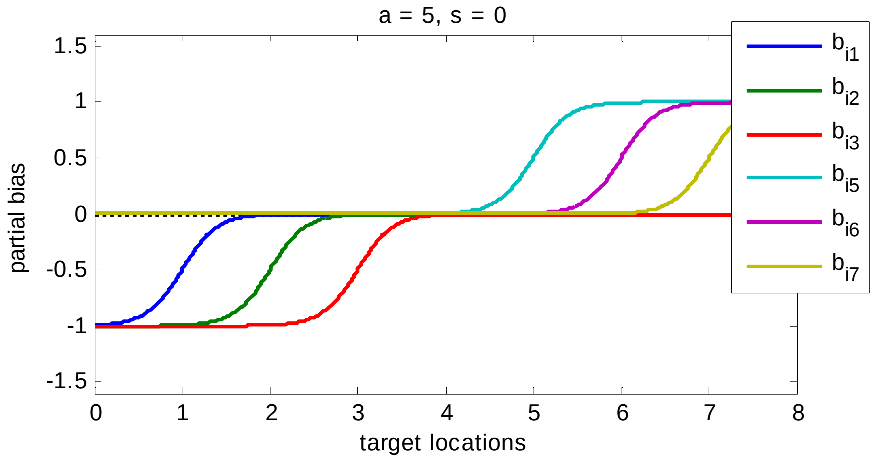

Figure 34 Example of of partial contextual biases induced by distractor-targets at locations #1,2,3,5,6,7 (i.e., for 1-7 context condition). Effect of particular spatial unit *j* on other spatial unit is weighted by sigmoidal neighborhood function shifted by *s* relative to location defined by spatial unit *j* with its shape affected by parameter *a*, and scaled by scaling factor *k*. Distractor is at location #4. The partial contextual biases are in the figure scaled to magnitude of 1.

The best fit of the model to the Exp 2 data is shown in Figure 35. Fit achieved using sigmoid neighborhood function was slightly worse compared to when the Gaussian function was used (on uniform space; compare Figure 35 with Figure 27; mse = 0.164 vs 0.107).

The best-fit value of parameter *s* was quite large, to examine it closer we plotted partial biases (on the figure scaled to absolute value of 1) induced by different distractor-targets units, see Figure 36. Large *s* and shallow shape of the function caused that partial biases on the examined region of space resemble those induced by Gaussian weighting functions (compare Figure 36 and Figure 28), suggesting that both variants of the model are heading towards one specific representation of the contextual effect in which distractor-targets affect larger region of space instead of only a small local region.

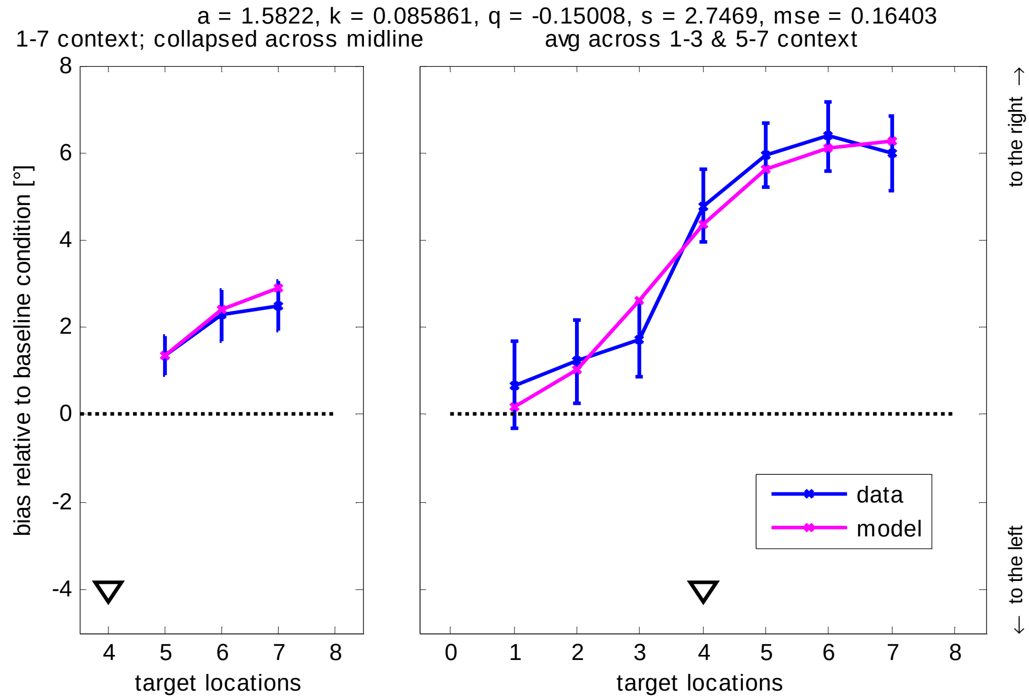

Figure 35 Comparison of the data of Exp 2 to the predictions of the sigmoidal-neighborhood uniform-space model with fitted parameters *a, k, q and s*. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse". In both panels data are depicted in such way that context is to the right side of the distractor.

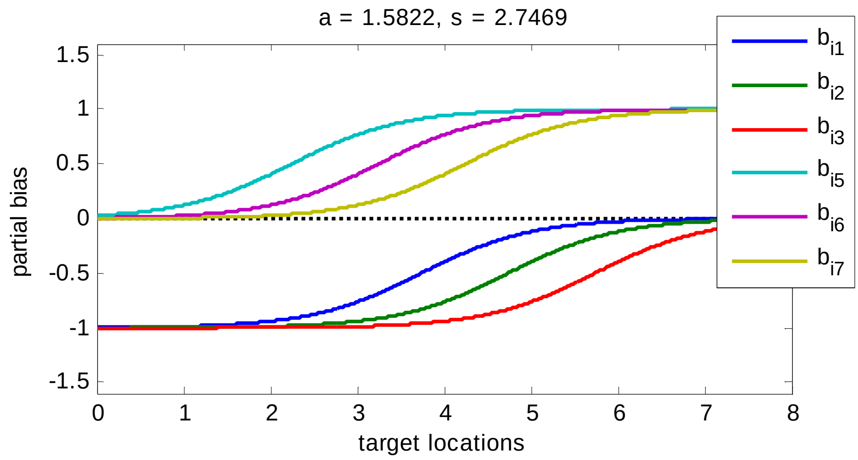

Figure 36 Partial contextual biases (scaled to magnitude of 1) induced by distractor-targets at locations #1,2,3,5,6,7 (i.e., for 1-7 context condition). Effect of particular spatial unit *j* on other spatial unit is weighted by sigmoidal weighting function shifted by *s* relative to location defined by spatial unit *j* with its shape affected by parameter *a*, and scaled by scaling factor *k*.

Best fit of the data from Experiment 1 is depicted on Figure 37 with partial contextual biases (scaled to <-1,1>) plotted on Figure 38. This variant of the model was considerably better in fitting the data than the sigmoidal model with non-uniform space (compare with Figure 32). Even though it did not fit all spatial patterns of the contextual bias properly (especially 1-3 context configuration), most of the trends are in the correct direction. The main source of error of the model is that similarly to Gaussian-neighborhood uniform-space model, given by how the model is designed, the biases for units #1-3 in 1-3 context configuration and units #5-7 in 5-7 context configuration are forced to be equal (reasons already discussed in one of the previous sections) while real biases are not. This suggests that additional factor influencing magnitude of the bias, for example the distance of the distractor-targets unit from the distractor location, can be considered in the model. However, standard errors of the means in the data for 1-3 context configuration are quite large (see errorbars of the left subpanel) suggesting that the plotted pattern might not persist after more measurements.

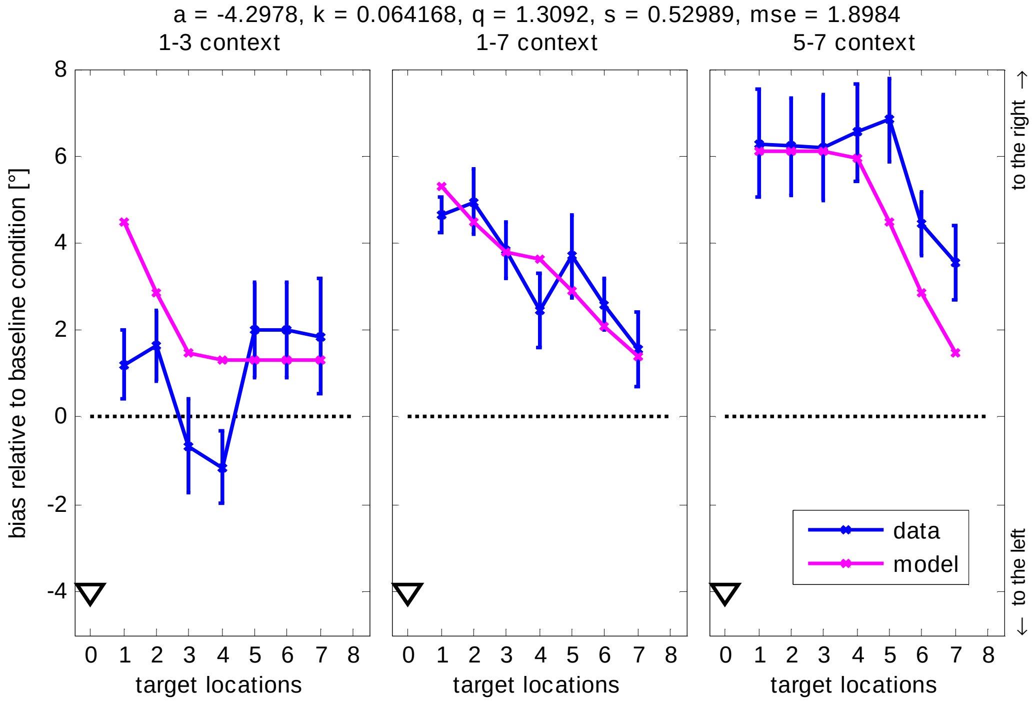

Figure 37 Comparison of the data of Exp 1 to the predictions of the sigmoidal-neighborhood uniform-space model with fitted parameters *a, k, q and s*. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse".

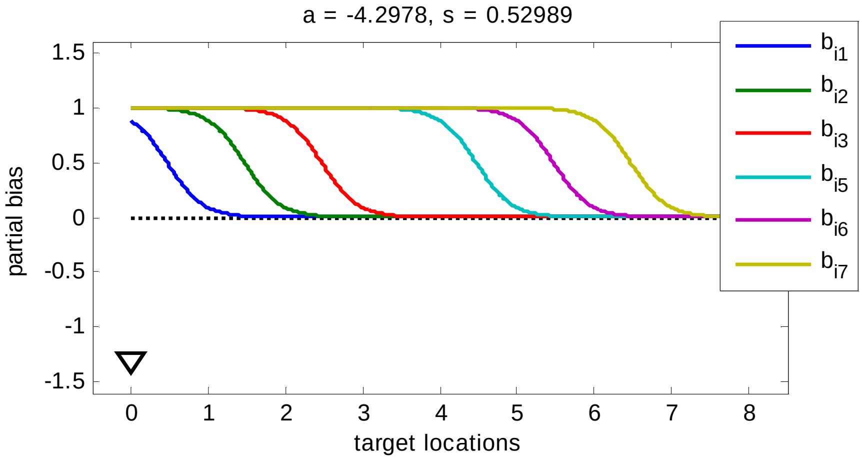

Figure 38 Partial contextual biases (scaled to magnitude of 1) induced by distractor-targets at locations #1,2,3,5,6,7 (i.e., for 1-7 context condition). Effect of particular spatial unit *j* on other spatial unit is weighted by sigmoidal weighting function shifted by *s* relative to location defined by spatial unit *j* with its shape affected by parameter *a,* and scaled by scaling factor *k*.

4.2.4 Model with sigmoidal weighting function and non-uniform space

Figure 39 shows the sigmoidal-neighborhood non-uniform-space model fitted to the data from Experiment 2. The match between the model and the data is overally the best among all variants of the model examined. The associated transformation of space is plotted on Figure 40, indicating that quite large manipulation with space was required to achieve the best fit.

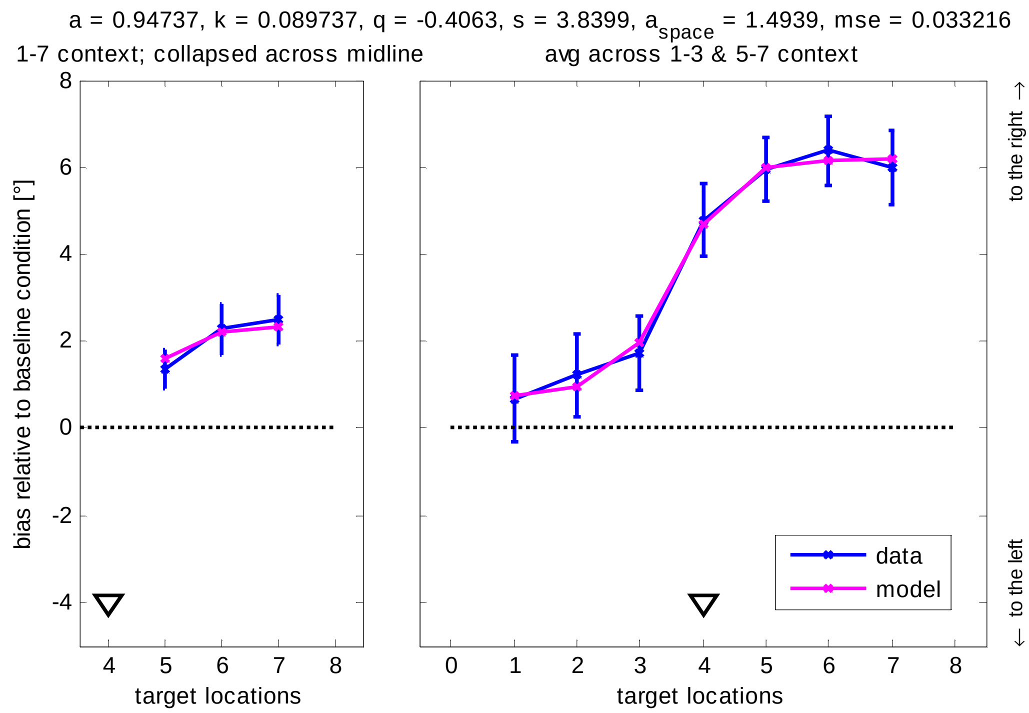

Figure 39 Comparison of the data of Exp 2 to the predictions of the sigmoidal-neighborhood non-uniform-space model with fitted parameters *a, k, q, s and a_{space}*. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse". In both panels data are depicted in such way that context is to the right side of the distractor.

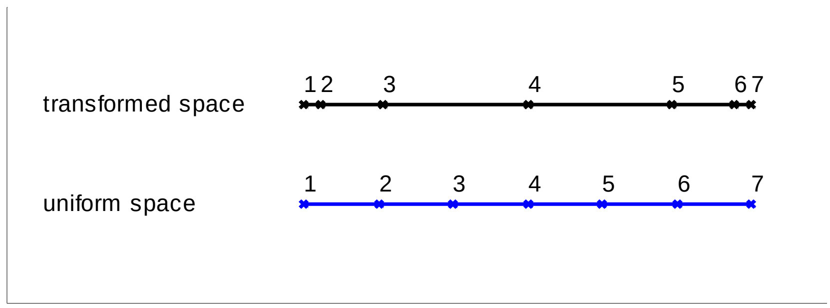

Figure 40 Transformation of space of space with best-fit value of parameter a_{space} = 1.4939 and rescaled to <1,7> compared to uniform space.

Figure 41 shows how the model performed in fitting the data from Experiment 1. The fit was comparable to the fit when no transformation was used (compare with Figure 37). In fact, the value of the parameter a_{space} suggests that the space was transformed only negligibly.

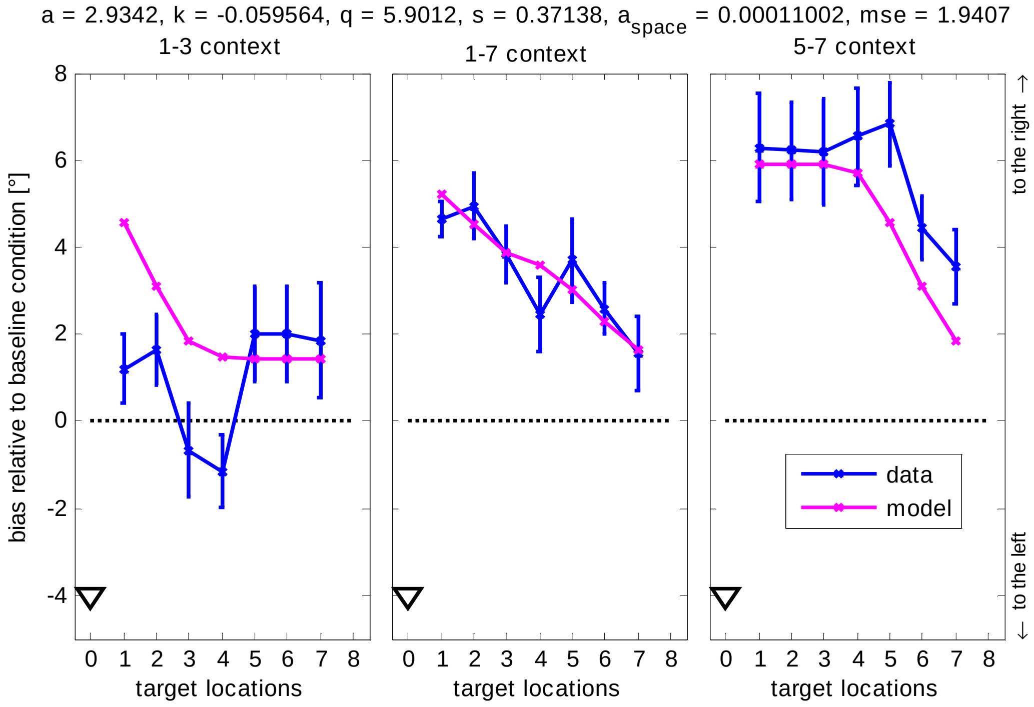

Figure 41 Comparison of the data of Exp 1 to the predictions of the sigmoidal-neighborhood non-uniform-space model with fitted parameters *a, k, q and* a_{space}. Best-fit model parameters are stated at the top of the figure, together with mean squared error "mse".

4.3 Summary

Table 2 and Table 3 shows summary of best-fit parameter values for different variants of the model tested and for different experiments. Both neighborhood models were able to describe data from Experiment 2. The sigmoidal-neighborhood model was able to describe also the data from Experiment 1, but with different values of parameters than for the Experiment 2.

Important aspect of the data was that the contextual bias depended also on distribution of no-distractor trials. Specifically, on whether the region between the distractor and the distractor targets (including) is "bounded" from the side by no-distractor targets or whether no stimuli are presented in direction in which the perception should be shifted (this was already discussed in section 3.5 Discussion of all experimental results). Other experiments should be performed in order to understand how and why the distribution of no-distractor targets affects the contextual plasticity. Implementation of the revealed factor into the model should enable the model to describe both experiments.

Currently tested variants of the model suggest that sigmoidal neighborhood is better in describing the results, supporting hypothesis H4. However, different transformations of space should be tested, or another factor which alters the contextual effect depending on the distance of the distractor-targets from the distractor location, should be implemented in the model to confirm this result.

Different neighborhood functions might provide even better results. In particular, neighborhood functions that affect only the space between the distractor and the distractor targets especially should be considered in future modeling.

		σ	k	q	a_{space}	mse
Gaussian uniform	Exp1	2.02	-0.02	4.31	-	4.90
	Exp2	2.08	0.10	-0.27	-	0.11
Gaussian non-uniform	Exp1	0.00	0.02	2.56	-9.03	4.77
	Exp2	2.81	0.09	-0.43	-1.11	0.05

Table 2 Summary of best-fit parameter values for Gaussian-neighborhood model.

		a	k	q	a_{space}	s	mse
Sigmoidal uniform	Exp1	-4.30	0.06	1.31	-	0.53	1.90
	Exp2	1.58	0.09	-0.15	-	2.75	0.16
Sigmoidal non-uniform	Exp1	2.93	-0.06	5.90	0.00	0.37	1.94
	Exp2	0.95	0.09	-0.41	1.49	3.84	0.03

Table 3 Summary of best-fit parameter values for sigmoidal-neighborhood model

5 Conclusion

5.1 Summary of results

The thesis examined dynamic processes in auditory spatial perception. Specifically it focused on the effect observed in [64] which was referred to as “contextual plasticity”. This effect suggests that localization of a target sound depends on context in which the listeners perform the localization task. The context is represented by an interleaved more complex localization task, in which the target sound is preceded by another sound (referred to as “distractor”) from a known location. We conducted two behavioral experiments examining various spatial aspects of this effect, in order to understand why this effect occurs and what its underlying neural representation is.

Spatial aspects manipulated in the experiments were: location of the distractor relative to the listener (azimuths 0°,±45° and ±90°), spatial configuration of the targets in distractor trials (to the one side of the distractor - either close to, or far from, the distractor; or to both sides of the distractor), tested region of space relative to the listener (region around frontal median plane; region around interaural axis; or region between frontal median plane and interaural axis).

The contextual effect induced in our experiments was very similar to what was observed in [64]. Presence of the contextual stimuli induced biases in responses on interleaved no-distractor trials. The magnitude of the contextual bias (relative to baseline condition in which no contextual trials were presented) was approx. 6° and its direction was from the distractor towards the distractor-targets locations. The effect build up very quickly after the onset of the distractor trials (within approx. 30 trials; i.e., approx. 2 minutes) and soon after its offset began to decay. In the following sub-sections we will describe the observed spatial aspects of the effect and summarize the results of the model of the contextual bias.

5.1.1 Experimental results

5.1.1.1 Effect of the distractor location relative to the listener

Effect of the distractor location relative to the listener was not consistent across experiments. In the Experiment 1, frontal distractor induced larger contextual biases than lateral distractor, while in the Experiment 2 no difference was found. The most probable reason is that even though the distractor was at the same locations relative to the listener in both experiments, remaining stimuli were presented from different location relative to the distractor, which might have caused the difference (in Experiment 1 the frontal/lateral distractor was at the side of the speaker array while in the Experiment 2 it was in its center). Thus, the effect of the distractor location is not clear yet and another experiments need to be performed.

5.1.1.2 Effect of spatial configuration of the targets in distractor trials

We found that the contextual bias depends on spatial configuration of distractor-targets. Distractor-targets presented only on one side of the distractor caused that responses to targets from this side were shifted away from the distractor, as if the space between the distractor and distractor-targets (including) was stretched towards the side. The magnitude of the bias was not uniform across all locations. Instead, it had more complicated spatial pattern. Importantly, responses to targets from the other side of the distractor remained unaffected by the context. From these off-context locations, only the negligible bias is observed at locations closest to the distractor, having the same direction as on the on-context side, and being a consequence of generalization of the effect from neighboring locations.

5.1.1.3 Effect of region around the listener

Magnitude of the effect did not depend on which region of space relative to the listener was tested. More importantly, effect induced at one side of the interaural axis did not generalize to locations on the other side of the distractor in an opposite direction. Instead, even though only negligible, bias in the same direction as on on-context side was observed, what suggests that it operates on later stages of processing at which the representation is assumed to be supermodal, most likely Cartesian (i.e., beyond the stage at which binaural localization cues, which use polar representation, are processed).

5.1.1.4 Contextual effect in other measures of localization performance than bias

If the measure of the localization performance was bias, the effect of context was mostly negative, shifting responses away from the actual target locations (but it depended on the context configuration and on how accurate were baseline responses). However, when considering other performance measures such as correlations of responses with actual target locations and standard deviation of responses for particular target location, the effect of context was positive – it increased the correlations and lowered the standard deviations of responses. Since listeners had their eyes closed during the experimental run, they might lose the visual anchors suggesting them where is the speaker array located and hence their responses were drifting in time towards the frontal locations. In distractor runs, repeated presentation of the distractor (and possibly also the distractor-targets) from the same location might act as an anchor, which, after initial inducing of biases, kept responses more stable and more correlated with actual target locations.

5.1.2 Model of the contextual bias

Simple computational model was proposed with a purpose to explain contextual bias observed in the experiments. The model describes the observed contextual biases for a specific region of space on the basis of spatial distribution of distractor-targets. Specifically, the model assumes that presence of distractor-targets at a particular location induces contextual bias at this and other locations defined by a neighborhood function (either Gaussian or sigmoidal). Neighborhood functions were chosen such that the biases would be induced more on the side of the distractor on which the distractor-targets were presented and not on the other side, according to what was observed in the experiments. Different variants of the model were tested (differing in neighborhood function and in whether they operate on uniformly distributed, or non-uniformly distributed spatial units), in order to examine how the contextual effect might be represented and in order to find simple description for our results.

The model was able to describe many characteristics of the data, for example that the context induced contextual biases more at the side of the distractor on which it was presented than on the other side, or that the effect had different magnitudes when context was presented on one side of the distractor compared to both sides of the distractor. However, some aspects of the data could not be explained by the model, such as the different magnitude of the effect on on-context locations when the context was near the distractor compared to when it was farther away from the distractor, or the dependency of the contextual effect magnitude on the distribution of non-context stimuli relative to the distractor. Thus, additional parameters or should be considered in the model, which would be able to describe these aspects of the data.

5.2 Note to the experiments

Some analyses of the experiments from this thesis were presented also in [96] and [97]. The experiments were conducted with the help of Jozef Peklanský and Daniel Husár, who presented their analyses in their diploma theses [72][73].

We conducted several other experiments examining different aspects of the contextual effect. Results were presented in [94] (temporal aspects) and [95] (dependency on distractor characteristics).

5.3 Possible cause of the contextual effect and its relation to other studies

In previous sub-sections, several aspects of the contextual effect were presented, its possible neural representation was discussed and its influence on localization performance was evaluated but it was not yet suggested why the effect occurs.

Our discussion about the cause of the effect will consider also results of the other experiments (not discussed in the thesis) we performed in order to study the different aspects of the contextual effect (even though not all of them statistically supported). Their results can be summarized as follows:

The contextual effect:

- tends to increase with increasing percentage of distractor trials within a run [94],
- at on-context region, it decreases with increasing distance of the target from the distractor [94] (consistent also with current study),
- is larger when the distractor stimulus and the target stimulus are spectro-temporally similar than when they are not similar [95],
- does not depend on whether in the distractor trials the distractor precedes or follows the target [95].

If we assume that the effect is caused by bottom-up mechanisms (induced by presentation of contextual stimuli affecting neural representation of space at some level), one of the possible explanations of the contextual bias might be that repeated activation of the same spatial position (by repeated presenting a distractor from same location) may fatigue its underlying neural representation (similarly to prolonged exposure to adaptor as observed in [24][25][26]) which would cause that locus of mean activity in the spatial map would shift away from the distractor, resulting in biases in responses (as described in Carlile et al. [24]). However, based on this, biases should be observed at both sides of the distractor (radial biases away from adaptor were observed in [24]), while in current study they occur only on the side on which the distractor-targets are presented. Hence, another explanation should be considered.

Our hypotheses from the Experiment 1 linked the effect with a change in listener's strategy. Specifically, that in the distractor trials, in which the localization of the target is difficult due to the preceding distractor and the perception of the target is shifted towards the distractor (resembling precedence effect conditions), listeners might try to overcome the shifts caused by the precedence effect and shift their responses away from the distractor. Since they did not know in advance whether a distractor trial or a no-distractor trial will be presented, they might keep this strategy throughout whole run in order to improve their performance (especially because most of the trials in a run were distractor trials). However, some of our predictions were not confirmed by the results, suggesting that the hypotheses or our assumptions are wrong. This hypothesis is also not supported by results from [95] which show that the effect is induced also when the distractor follows, instead of precedes, the target (on the other hand, even the first sound might be difficult to localize).

Other possible explanations of the observed contextual effect could be that it is only a prolonged effect of a distracting sound which affects stimuli within a time window which includes also no-distractor trial. If after the interval within which a precedence effect occurs, the distractor repulses responses instead of attracting them, it could cause observed biases. Since the number of distractor trials (75%) was much higher than the number of no-distractor trials (25%) and both types of trials were interleaved, most of the no-distractor trials were in fact preceded by distractor trial. However, this explanation is also not consistent with our results, because the biases should be observed on both sides of the distractor, not only on the side at which the context is presented.

One of the important questions related to contextual effect is on which level of processing it takes place - if the perception itself is changed or only mapping from perception to motor reaction (pointing to perceived location). Getzmann et al. [27] examined whether the methods of responding, specifically verbal responding vs. manual pointing, affect the localization of targets presented continuously with / or successively after the “frames” (acting similarly to distractor in our study) in vertical dimension, but no differences were found, suggesting that such areas are affected by the context which guide both these methods of responding [27].

Plasticity in our study was induced quickly, within few minutes. Rapid adaptation was observed in many other studies, for example when adaptation was induced by misleading feedback [22][23] or in ventriloquism aftereffect [87] (not mentioning studies of exposure to adaptor). Our results confirm that auditory spatial processing is dynamic on very short times scales.

Another relevant studies are studies of precedence effect build-up. The precedence effect normally occurs if the two successive sounds are presented with a specific delay between them. However, if the two stimuli with the delay too long to normally induce a precedence effect are repeatedly presented several times, the precedence effect is able to build up also on these longer delays ([74], or review in [71]). However, responses in our study were biased away from the distractor (and not towards as they would be in the precedence effect).

Overally, the contextual effect is in some aspects similar to what was observed in other adaptation studies. However, in order to understand the cause of the effect, other its aspects need to be studied.

5.4 Aims fulfillment and thesis contribution

The following text presents the list of aims and summarizes their fulfillment.

- **Design of behavioral experiments which will examine spatial aspects of the “contextual plasticity” phenomenon, observed in [64].**
    - Two experiments were designed in which spatial properties of the stimuli were manipulated in a desired way to study the contextual effect. The design is described in the chapter 3 Experimental part, in methods sections). Experimental procedure for presentation of

the stimuli and data collection was written in MATLAB. This environment was also used for data preprocessing, analysis and visualization.

- **Evaluation of the contextual effect and of its dependence on specific spatial manipulation of the contextual stimuli.**
  - Contextual effect was evaluated in several measures: as a bias relative to baseline localization, and in terms of standard deviations in responses and correlation of responses with actual target locations. Results were subjected to analysis of variance to identify important factors. Analyses of the effect and its dependencies on spatial manipulations of stimuli are summarized in chapter 3 Experimental part (in results and discussions subchapters).
- **Design of a quantitative model of contextual bias based on observed results.**
  - Based on the observed spatial patterns of the contextual bias a model was designed, which computes the contextual biases according to spatial distribution of the contextual stimuli. The mechanism on which the model is based in described in the chapter 4 Model of contextual bias (Introduction section). The model was implemented in MATLAB.
- **Evaluation of the model on the observed data.**
  - Different variants of the model tested evaluated in how accurately they describe the observed data. Results are presented in chapter 4 Model of contextual bias (section 4.2 Results).
- **Discussion of the results with other related studies of plasticity in sound localization**
  - Results of the experiments are summarized and put into context of several other adaptation studies in the subchapters 5.1 and 5.3

The contribution of the thesis can be summarized into these points:

- **Describes spatial aspects of a phenomenon referred to as "contextual effect" which was observed in [64]**: it quantitatively evaluates the effect of the configuration of the contextual stimuli, location of the distractor relative to the listener and other spatial manipulations of the stimuli.

- **Proposes a model of the contextual bias based on observed results**
- **Offers contribution to methodology** for other spatial hearing experiments, since it describes specific example of spatial and temporal interactions between the stimuli (by showing how response in a particular trial might be affected by context of other task/stimuli in previous trials)

5.5 Suggestions for further research

In addition to the spatial aspects studied in this thesis, the contextual effect needs to be studied from many other aspects in order to fully understand why it occurs. Regarding analyses most related to currently presented results, we propose several suggestions. For example, it should be evaluated whether the context has positive effect on mapping between responses and actual target locations also in Experiment 1. Also, effect of the distribution of the non-context stimuli needs to be examined, since it seems to affect the magnitude of the contextual bias. Moreover, the model of the contextual bias should be also improved to fully describe the contextual bias (for example by implementing factor which alters the contextual effect depending on the distance of the distractor-targets from the distractor location, or by using different neighborhood functions).

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