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Contextual plasticity in sound localization: characterization of spatial properties and neural locus

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Summary
Localization of a target sound can be affected by context in which the task is performed. A previous study [Kopco et al., JASA, 121, 420-432, 2007] showed, for broad-band noise stimuli, that interleaving the target-only trials with trials in which the target is preceded by distractor from fixed location causes biases in responses on target-only trials away from the distractor. Here we examined how the effect depends on the spatial distribution of stimuli, on availability of visual signals, and on response method used, in order to understand the nature of its underlying neural representation. Using methods similar to the previous study, we performed three experiments in which we varied 1) spatial configuration of the contextual distractor and target stimuli, 2) the examined locations of the target-only stimuli, and 3) the response method used by the subjects. Response biases and standard deviations on target-only trials were evaluated. The context biased responses away from the distractor. The effect generalized to locations at the same side of the distractor as the contextual stimuli (but not to those on the other side), stretching the space away from the distractor. The presence of context also reduced response variability, but only when the contextual stimuli spanned a subregion of the target-only test region. This suggests that the repeated presentation of the context might increase spatial perceptual sensitivity for targets presented in the region covered by the context. Effect of the context on biases and variance in responses was roughly independent of the response method or of availability of the visual signals. Thus, contextual plasticity is caused by changes in auditory spatial processing only. [Supported by VEGA-1/0492/12 and APVV-0452-12].

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1. Introduction

Many studies show that localization of a sound can be influenced by other sounds, either simultaneous [1] or preceding the target [2]. Well-described *precedence effect* illustrates that the extent of this influence depends on the temporal proximity between the target and preceding sound, being largest for interval of approx. 1-5 ms (depending on type of the stimulus) and disappearing with increasing delay between the two sounds (for a review, see [3]). Short-term interactions between two sounds were studied also in [4]. In the experiment, subjects localized a target sound which was in some trials preceded by a distractor from a fixed and *a priori* known location. Interestingly, in addition to the effect of immediately preceding distractor, another effect was observed – responses on interleaved control

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trials in which no distractor was presented were biased depending on the distractor location, suggesting that localization of a target can be affected by the context of other trials in the experimental run (i.e., trials with distractor). This effect was referred to as *contextual plasticity*.

Our previous studies of this effect show that it depends on the frequency of occurrence of the trials with the distractor [5] and on spectro-temporal similarity of the target and the distractor [6].

In order to understand the neural representation on which the effect operates and its locus in the processing pathway, the current study presents the results of three experiments that examined 1) spatial characteristics of the contextual effect (forms of generalization of the effect to "unadapted" locations and dependency on spatial distribution of the contextual- and non-contextual stimuli) and 2) how non-auditory factors affect the contextual effect (involvement of visual and motor areas in the contextual effect).

The experiments tested several hypotheses, e.g., that the spatial distribution of the distractor and targets in trials with distractor (referred to as "distractor-targets") will affect the magnitude and the spatial distribution of the contextual effect. We expected that the effect will, at least partly, generalize also to locations at which no distractor-targets were presented. Since in previous studies the context biased responses away from the distractor, we expected that presenting the distractor-targets on both sides of the distractor will induce no contextual effect since the biases from the opposite sides will cancel-out (H1). We also expected that magnitude of the contextual effect will depend on the position of the tested region of space relative to the subject due to different acuity of underlying spatial representation (H2).

One of the possible explanations of the effect might be that due to very short distractor-to-target SOA it is difficult to spatially separate the target and the distractor. In order to better localize the target, subjects focus their attention away from known distractor location (or perceptually push the target away from distractor location), which might affect their responses also on interleaved no-distractor trials, giving rise to the contextual bias. We hypothetize that presenting the distractor-targets close to the distractor will induce larger contextual effect than presenting distractor-targets far from the distractor because in the first case it is more difficult to separate the target from the distractor (H3).

In order to make sure, that the contextual effect occurs in auditory processing and is not related to an adaptation in motor areas, and in order to test its dependency on visual signals available, we tested different methods of responding (hand-pointing with eyes closed, hand-pointing with eyes open, responding by typing the perceived location on a keyboard). We hypothetised that the contextual effect will be observed in each of the conditions (H4). However, we expect that the contextual effect will be larger when no visual signal will be available because there will be no visual reference for "anchoring" the internal spatial representation (H5).

In addition to causing biases in sound localization, the contextual effect might affect localization also in other ways. Based on the results of previous study we expect that it might decrease the response variability (H6) since distractor might act as an anchor, making responses more stable.

2. Methods

Three experiments were performed, Experiment 1 and Experiment 2 focusing on spatial aspects of the contextual effect and Experiment 3 on influence of availability of visual signals and response method used on the contextual effect. Partial results of Experiment 1 presented here were already presented in [7].

2.1. Experiment 1

Similar design to the one in [4] was used. Subject was surrounded by an array of 7 loudspeakers separated by 11.25° (see Fig.1), placed 1.1 m away from the subject. His/her task was to localize a target sound presented on each trial randomly from one of the loudspeakers. In some trials (referred to as "distractor trials"), target was preceded by distractor sound presented from the central loudspeaker.

Both the target and the distractor sounds were identical 2-ms frozen noise bursts. The distractor-to-target onset asynchrony was set to 25 ms. Experiment consisted of 4 approx. 1.5-hour long sessions. Each session consisted of experimental runs and a baseline run:

1) In the experimental runs, two randomly interleaved types of trials were used – trials in which only the target was presented (referred to as no-distractor trials and representing 25% of trials) and trials in which the target was preceded by the distractor (referred to as distractor trials and representing 75% of trials).
2) Baseline run consisted of only no-distractor trials and was used as a reference for computation of the contextual effect.

In order to examine the spatial properties of the contextual effect we varied: 1) position of the speaker array relative to the subject (around median plane, around left/right lateral plane), 2) spatial configurations of targets in distractor trials (1-3 context, 5-7 context and 1-7 context, representing restriction on presentation of targets in distractor trials to locations #1-3, locations #5-7, locations #1-3&5-7, respectively, see Fig.1).

Targets in no-distractor trials could be presented from each of the 7 possible target locations (including central speaker #4)

Ten normal-hearing subjects participated in the experiment. Subjects responded by handheld pointer and they were instructed to have their eyes closed during the experimental runs.

2.2. Experiment 2

The setup used in the Experiment 2 was similar to Experiment 1, except that speaker array had one distractor speaker added at each side of an array (i.e., 9 speakers altogether with 3 possible distractor locations) and spanned locations 0° to +/-90° (see Figure 1).

Manipulated factors were: 1) orientation of speaker array relative to the subject (left, right half of the frontal horizontal plane), 2) location of the distractor (frontal: 0°, intermediate: +/-45°, lateral: +/-90°), and 3) spatial configuration of targets in distractor trials (1-3 context, 5-7 context, 1-7 context, see Fig.2)

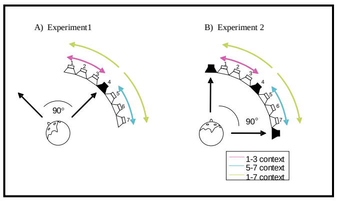

Figure 1 Experimental setup for the Experiment 1 (panel A) and for the Experiment2 (panel B). Possible target locations are indicated by labeled loudspeakers. In both experiments, on no-distractor trials, target could be presented at each of the 7 locations. On distractor trials, targets were restricted to a subset of locations indicated by colored arc above the loudspeakers, giving rise to three context cofigurations referred to as: 1-3 context, 5-7 context and 1-7 context condition (locations #1-3, #5-7 and #1-3&5-7, respectively). Black speakers indicate possible distractor locations (only one of them used in each particular run). Black arrows indicate possible orientations of the listener relative to the speaker array.

Experiment consisted of 6 approx. 1.5 hour- long sessions. Eight normal-hearing subjects participated in this experiment.

2.3. Experiment 3

In this experiment we examined the non-auditory aspects of contextual plasticity. The setup was similar to Experiment 2 except that the distractor was always frontal and distractor-targets could be presented from each of the 7 target speakers. Loudspeaker array was hidden behind the acoustic cloth. Above it was a paper arc labeled with letter-number pairs (spaced 1° and extending 10° to each side of an array) used for the indication of perceived azimuth in one of the conditions.

Manipulated factors were: 1) orientation of subject (left/right half of the frontal median plane), 2) method of responding (pointing with eyes closed, pointing with eyes open, typing an azimuth-corresponding label on a keyboard).

Experiment consisted of 4 sessions. Ten normal-hearing subjects participated in the experiment.

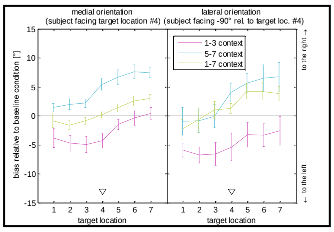

Figure 2 Contextual biases for medial orientation (left panel) and lateral orientation (right panel) of the speaker array relative to the subject, as a function of target location. The triangle indicates the distractor location.

2.4. Data analysis

From each condition, only no-distractor trials were considered in the analysis. In order to determine the effect of the context, the difference between the conditions with context and baseline condition was computed. The difference will be referred to as „contextual effect“.

We performed two types of analysis: 1) biases in responses and 2) standard deviation of responses.

In order to compare standard deviations across different conditions, number of data used for computation of the standard deviation were balanced across the conditions (by computing mean of 50 standard deviations, each computed from a pseudo-random sample from a baseline condition).

Data were collapsed across left-right lateral orientation since they were approximately symmetrical.

All plots show the across-subject means and across-subject standard errors of the means. All reported ANOVAs are Repeated measures ANOVAs with Box-Geisser-Greenhouse corrections.

3. Results

3.1. Spatial aspects of the contextual effect

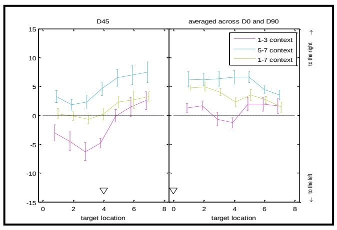

Figure 3 Contextual biases for distractor at 45 degrees re subject's straight ahead (left panel) and for data averaged across distractor at 0 and 90 degrees with x-axis showing the target location re. the distractor location (right panel)

3.1.1. Contextual effect in response biases

Figure 2 shows contextual biases as a function of target location when the speaker array was centered at subject's median plane (left panel) and at lateral plane (right panel). The same pattern of biases was observed for both orientations of the speaker array relative to the subject.

Context induced biases away from the distractor. The biases were observed at the side of the distractor from which the distractor-targets were presented (i.e., at "on-context" locations). No or only negligible biases (in the same direction) were observed on the other side of the distractor (i.e., at "off-context locations"; red line separates from baseline at locations #1-3 but not at #5-7, blue line separates at locations #5-7 but not at #1-3).

Context presented on both sides of the distractor induced only negligible contextual bias (green line close to zero).

These observations were supported by three-way ANOVA with factors of Context configuration (1-3 context, 5-7 context and 1-7 context), target locations (1,…,7) and orientation (medial, lateral) which revealed significant main effect of context configuration ($F_{2,18}$=30.19, p<0.01) and significant main effect of target location ($F_{6,54}$=15.6, p<0.01).

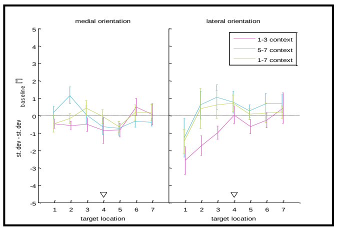

Figure 4 Contextual effect in standard deviations (i.e., difference between SD in a conditon with context and SD in baseline) for medial orientation (left panel) and lateral orientation (right panel).

Figure 3 shows the contextual biases from the Experiment 2. Centering the speaker array at 45 degrees re. subject's straight ahead and keeping the layout the same as in Experiment 1 resulted in the same contextual biases as observed in the Experiment 1 (compare left panel of Figure 3 with Figure 2). Distractors located at the side of an array (either at 0 degrees or at 90 degrees relative to straight ahead; right panel in Figure 3) enabled examination of generalization of the effect to locations at the same side of a distractor as the distractor-targets stimuli. Contextual bias for 1-7 context condition (yellow line) was largest for targets near the distractor (around 5 degrees) and decreased with increasing distance from the distractor. Similar decreasing pattern (but of different magnitudes) was observed also at on-context locations of 1-3 context and 5-7 context conditions. For 5-7 context, the bias clearly generalized also to off-context locations (#1-4), but for the 1-3 context the generalization is less clear due to both smaller magnitude of contextual bias in general and also more complicated spatial pattern (see pink line at locations #5-7).

3.1.2. Contextual effect in variability of responses

Standard deviation of responses (SD) was higher for azimuths closer to lateral plane (5-6 degrees for medial orientation versus 8-10 degrees for lateral orientation, data not shown). Figure 4 shows the contextual effect in SDs as a difference between SD of a particular condition with context and SD of baseline. Data from behind interaural axis were excluded from the analysis because accuracy of responding was in general very low at this region (subjects tended to respond always at approx. distractor location and not behind it). For the remaining subregions, the following pattern can be observed: Context restricted to subregion of space decreased SDs at the on-context locations (locations #1-3 for pink line and locations #5-7 for blue line are below zero), while no effect was observed at off-context locations (#5-7 for pink line and #1-3 for blue line) or when context was presented on both sides of the distractor (yellow line). Three-way ANOVA with factors of subregion (left medial, right medial, in front of inter. axis), target-context spatial coincidence (ON-context, OFF-context, ON-context-all, baseline) and distance from the distractor (1-3) revealed significant main effects of subregion ($F_{2,18}$=28.84, $p<0.01$), target-context spatial coincidence ($F_{3,27}$=4.97, $p<0.05$) and distance from distractor ($F_{2,18}$=4.87, $p<0.05$). Main effect of subregion is caused by worse SDs for subregion near interaural axis. Main effect of distance from the distractor suggests that SDs decrease for targets farther away from the distractor (or, from the other point of view, from the center of the speaker array), however, the magnitude of the decrease is only approx. 1 degree. Finally and more importantly, main effect of target-context spatial coincidence shows that standard deviations improved only in subregion in which the context was presented.

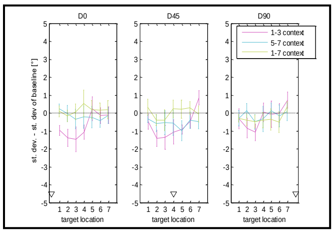

Figure 5 Contextual effect in standard deviations for the three distractor locations (in separate panels).

Figure 5 shows the contextual effect in SDs from Experiment 2. Again, SDs tend to decrease at ON-context locations – however, this effect was clearly observed only when on-context region was near median plane, not near lateral plane (compare pink and blue line). Consistent with results of Experiment 1, context distributed across whole speaker array did not affect SDs.

The dependency of the contextual effect on presence/absence of contextual stimuli within a particular subregion was supported by the results of four-way ANOVA with factors of orientation (facing left-most speaker, facing right-most speaker), distractor location (frontal, intermediate, lateral), target-context spatial coincidence (ON-context, OFF-context, ON-context-all) and target location (#1,2,3,5,6,7), which revealed significant main effect of target-context spatial coincidence ($F_{2,14}$=7.16, $p<0.05$) and no other significant main effect or interaction.

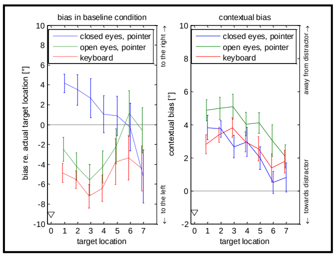

Figure 6 Bias relative to actual target location in baseline condition (left panel) and contextual bias (right panel) for the three response methods.

3.1.3. Preliminary discussion

Consistently with hypothesis H1, presenting the context on both sides of the distractor induced no or only negligible contextual bias. Since generalization of the effect “across” the distractor was not observed in such extent, this observation might be due to following reason: Since the total number of distractor trials was kept constant across conditions with context, restricting the number of locations used for presentation of distractor-targets resulted in more frequent presentation of distractor-targets per speaker in half-range conditions compared to whole range conditions. This might result in stronger adaptation, as already suggested in [5].

However, no effect of position of the tested region relative to the listener was found (not consistent with H2) suggesting that spatial acuity of the underlying structure does not influence the contextual effect or that the effect is induced in a structure with uniform spatial acuity.

Interestingly, contextual bias generalized (with the same magnitude) to locations between the distractor and the distractor-targets. In general, contextual bias for distractor-targets far from the distractor was even larger than the one for distractor-targets close to distractor (not consistent with H3). This suggest a kind of “stretching” of inner spatial representation between the distractor location and distractor targets locations.

Contextual effect also decreased the variability of responses in the part of the space where the distractor-targets were presented. However, this was observed only in case the contextual stimuli were restricted to a smaller spatial region and not when they were distributed across the whole tested region (only partially consistent with H6). This might be caused by more frequent presentation of distractor-targets per location in half-range context condition compared to whole-range context condition, as was already explained for contextual biases.

To summarize, presence of the contextual stimuli biased the spatial representation but on the other hand it improved resolution of the underlying part of the space.

3.2. Non-auditory aspects of the contextual effect

Consistently with previous experiments, baseline responses in “closed eyes, pointer” condition were skewed towards the center of the response range (see Figure 6, blue line has positive bias for target locations #1-3 and negative bias for target location #7). On the other hand, with eyes open, the response range was either stretched, when using pointer (green line has negative bias for target locations #1-5) or shifted, when using keyboard (approx. constant negative bias for red line).

Even though localization in general depended on response method used, contextual bias was roughly independent of it (right panel of Figure 6) with only slight tendency of the “open eyes, pointer” to cause larger contextual bias than the other two methods.

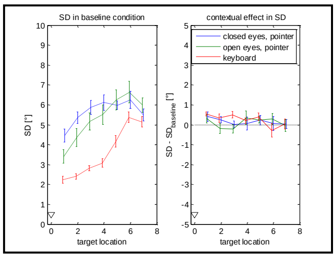

Figure 7 Standard deviation of responses in baseline condition for the three response methods as a function of target location (left panel) and contextual effect in standard deviations (i.e., a difference between SD of particular condition with context and SD of baseline condition)

3.2.1. Contextual effect in variability of responses

SDs of responses for all three response methods increase with laterality (except for the slight decrease at the edge of the speaker array). Lowest SDs, approx. 2-5 degrees, were observed for the keyboard condition, while SDs of the two pointing conditions were approx. 1-3 degrees higher (left panel of Figure 7).

Even though response method influenced accuracy of responding, it did not influence the contextual effect, which was for all three cases negligible (right panel of Figure 7).

3.2.2. Preliminary discussion

Method of responding affected localization responses. Responding by keyboard can be considered as the most precise of the three tested methods, due to the fact that 1) responses were only shifted (roughly) relative to actual target locations, while for other two methods more complicated transformations of space were observed, 2) variability of responses was significantly smaller than when the pointer was used.

However, response method did not affect the inducement of the contextual effect (consistent with H4). The fact that the contextual biases were induced also in case of keyboard response method suggests that the plasticity occurs on auditory rather than motor spatial representation. Availability of visual signals did not reduce the contextual effect (not consistent with H5). These results suggest that contextual effect seems to be caused purely by auditory processing.

4. Conclusion and overall discussion

In Experiments 1 and 2, presence of the contextual stimuli affected localization performance in both examined measures, biases and standard deviations. First, it induced biases in responses in direction away from the distractor, which generalized also to locations between the distractor and distractor-targets, but not to the locations on the other side of the distractor (re. location of the distractor-targets). Second, it decreased the variability of responses in the subregion in which the distractor-targets were more frequently presented, suggesting that some improvement of spatial resolution might occur for frequently stimulated (or task-relevant) spatial locations.

Results suggest that contextual plasticity is induced in a structure involved in auditory (rather than motor) processing. If the contextual bias occurred at earlier stages of auditory processing (on ITD/ILD map), presenting contextual stimuli on one side of the interaural axis would induce symmetric contextual bias also at the opposite side (e.g., bias induced at location 10 degrees in front of interaural axis would generalize to the location 10 degrees behind interaural axis) because symmetric locations re. interaural axis are in ITD/ILD maps represented by the same neural structure (share the same ITD/ILD). Since no symmetric generalization of bias across interaural axis was observed, contextual effect probably arises at later stages of auditory processing, in a structure with topographic-like spatial representation (for more details, see [7]).

Observed contextual biases could be described by a model which assumes that the distractor-targets induce local biases in the topographically organized spatial map (as proposed in [7]). Extent to which presentation of a distractor-targets at particular location affects inducement of contextual bias at neighboring locations would be given by a neighborhood function. Simple Gaussian function centered at each distractor-targets location would not be sufficient to describe all the data since the pattern of the contextual bias was more complicated (i.e., generalization also to locations between the distractor and distractor targets). Sigmoidal function might be more appropriate, however, its relation to known physiology must be considered.

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