

The Extent of Task Specificity for Visual and Tactile Sequences in the Auditory Cortex of the Deaf and Hard of Hearing

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It has been proposed that the auditory cortex in the deaf humans might undergo task-specific reorganization. However, evidence remains scarce as previous experiments used only two very specific tasks (temporal processing and face perception) in visual modality. Here, congenitally deaf/hard of hearing and hearing women and men were enrolled in an fMRI experiment as we sought to fill this evidence gap in two ways. First, we compared activation evoked by a temporal processing task performed in two different modalities, visual and tactile. Second, we contrasted this task with a perceptually similar task that focuses on the spatial dimension. Additional control conditions consisted of passive stimulus observation. In line with the task specificity hypothesis, the auditory cortex in the deaf was activated by temporal processing in both visual and tactile modalities. This effect was selective for temporal processing relative to spatial discrimination. However, spatial processing also led to significant auditory cortex recruitment which, unlike temporal processing, occurred even during passive stimulus observation. We conclude that auditory cortex recruitment in the deaf and hard of hearing might involve interplay between task-selective and pluripotential mechanisms of cross-modal reorganization. Our results open several avenues for the investigation of the full complexity of the cross-modal plasticity phenomenon.

Key words: auditory cortex; cross-modal perception; deaf; fMRI; plasticity

Significance Statement

Previous studies suggested that the auditory cortex in the deaf may change input modality (sound to vision) while keeping its function (e.g., rhythm processing). We investigated this hypothesis by asking deaf or hard of hearing and hearing adults to discriminate between temporally and spatially complex sequences in visual and tactile modalities. The results show that such function-specific brain reorganization, as has previously been demonstrated in the visual modality, also occurs for tactile processing. On the other hand, they also show that for some stimuli (spatial) the auditory cortex activates automatically, which is suggestive of a take-over by a different kind of cognitive function. The observed differences in processing of sequences might thus result from an interplay of task-specific and pluripotent plasticity.

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Introduction

Previous evidence shows that the visual cortex in the blind and the auditory cortex in the deaf can become engaged in other kinds of sensory processing (Heimler et al., 2015). In the deaf, the auditory cortex is activated by a range of visual tasks: visual motion (Shiell et al., 2016), change detection (Bottari et al., 2014), peripheral vision (Bavelier and Neville, 2002), and vibrotactile processing (Karns et al., 2012). Which mechanism governs these cross-modal changes is still under debate. The task-specific principle asserts that in such cases the function of a given area is preserved although its input modality switches. In support of this view, several studies have shown that higher-order “visual”

areas maintain their category-selective functions in the blind (Amedi et al., 2017).

Examples of analogous task-specific brain reorganization in the auditory cortex in deafness come primarily from animal studies. In deaf cats, auditory areas involved in peripheral sound localization are recruited when perceiving peripheral visual stimuli (Lomber et al., 2010, 2011). Recently, however, two papers have demonstrated an analogical mechanism in the auditory cortex of deaf humans (Benetti et al., 2017; Bola et al., 2017).

The two aforementioned works found that exactly the same part of the auditory cortex is recruited by visual-rhythm discrimination tasks in deaf subjects and by auditory-rhythm discrimination tasks in hearing subjects (Bola et al., 2017); also, the voice-related auditory area preserves its particular function of identity recognition and becomes involved in face perception in deafness (Benetti et al., 2017). Both are instances in which the sensory input of a given auditory region is switched, but its typical functional specialization is preserved. On the basis of these results, functional specificity could be seen as a general rule that also governs cross-modal reorganization outside the visual cortex.

However, the task-specific brain reorganization hypothesis is not fully agreed on as it fails to explain how deprived cortices assume new, higher cognitive roles. Substantial evidence from studies on the blind shows that the visual cortex can be engaged in general language processing (Bedny et al., 2011; Lane et al., 2015), mathematical reasoning (Kanjlia et al., 2016), and nonverbal executive functions (Loiotile and Bedny, 2018). Moreover, a few recent studies indicate that the auditory cortex can exhibit similar flexibility and engage in higher cognitive functions, such as working memory (Ding et al., 2016; Twomey et al., 2017; Cardin et al., 2018) and executive functions (Manini et al., 2021).

The take-over of the deprived cortex by higher-cognitive functions and the principle of task specificity could be reconciled to a certain degree (Cardin et al., 2020). The key questions would then be: what is the extent of functional selectivity and what are its limits? In this context, evidence concerning cross-modal plasticity from the two aforementioned experiments is scarce. First, since both were limited to the visual modality, it remains unclear whether the same mechanisms of plasticity could be valid for tactile processing. Second, our previous experiment (Bola et al., 2017) tested only one specific behavioral function (rhythm discrimination), which was compared against passive observation of temporally regular stimulation. This raises the question of whether the observed effect is related to the particular character of the task or rather reflects general attentional engagement.

Here, we aimed to illuminate this issue: first, by studying the same rhythm processing task in two modalities (visual and tactile); second, by comparing the specific behavioral function in question (temporal sequence discrimination) with a perceptually similar task performed on the spatial aspect of the same stimuli (spatial sequences discrimination).

A group of congenitally deaf or hard of hearing and hearing subjects was enrolled in an fMRI experiment during which they performed a temporal and spatial sequences discrimination task in visual and tactile modalities. In line with the task-specific hypothesis, we anticipate that the effect of cross-modal reorganization within the auditory cortex in deaf and hard of hearing individuals should be consistent across different modalities while being selective to one type of task.

Materials and Methods

Participants

In the present study, congenitally deaf or hard of hearing and hearing subjects were enrolled in an fMRI experiment. Twenty-one congenitally deaf and hard of hearing adults (10 females, mean age = 29.3, SD = 6.9, average length of education = 14.5 years, SD = 2.0 years) and 21 hearing adults (10 females, mean age = 25.8, SD = 5.45, average length of education = 14.9 years, SD = 2.0 years) participated in the experiment. Twelve of these participants took part in our previous experiment (Bola et al., 2017). The deaf or hard of hearing and the hearing subjects were matched for gender, age and years of education (all $p > 0.05$). All subjects were right-handed; they had normal or corrected-to-normal vision and no neurologic deficits. All hearing subjects had no known hearing deficits. All deaf and hard of hearing subjects reported being profoundly and congenitally deaf (hearing loss >90 dB, with diagnosis of profound or absolute deafness; for more information, see Tables 1, 2). However, some of them reported they are able to understand speech using hearing aids without lip-reading (Table 1). On this basis, we refer to the group of participants as deaf and hard of hearing individuals.

The deaf and hard of hearing participants did not use cochlear implants; 9 participants reported using hearing aids on a daily basis at the time the experiment was conducted; three of them reported understanding speech well when using hearing aids, although only one of them reported understanding well without lip-reading (Table 1). All deaf and hard of hearing participants were proficient in Polish Sign Language (PJM); they reported communicating in this language on an everyday basis since childhood and indicated PJM as their main method of communication in adulthood (Table 2). Most participants reported good or fluent PJM proficiency and assessed their Polish speech proficiency as poor or moderate. During the MRI session, the sign language interpreter communicated with participants using a webcam. Before the experimental session, all instructions, questionnaires, the safety survey and the consent were translated into PJM.

All participants used protective headphones during the MRI scanning.

Experimental task

The experimental design involved two types of stimuli (stimulus dimensions), temporal and spatial; two sensory modalities, tactile and visual; and task versus no-task, i.e., passive observation (Fig. 1).

The temporal task was directly based on our previous study (Bola et al., 2017) and consisted of discriminating between a pair of complex rhythmical sequences (Fig. 2A, left). In the visual version of the task (visual temporal sequences), subjects were presented with sequences of two briefly flashing small white discs (1.1° radius) connected to each other in the center of the screen. In the tactile version of the task, vibrating pulses were delivered to four fingers on both hands using a custom-made piezoelectric device (Neurodevice). Visual and tactile temporal stimuli were presented in a random combination of short or long periods of time (50 or 200 ms) for two sequences of six stimuli, with 100-ms gaps between each presentation.

For the spatial task, perceptually similar stimuli (Fig. 2A, right) were repeatedly presented for the same period of time (125 ms), with the following modification: only one of the circles (either the left or right side of the screen) was filled, while the other one was empty. In the tactile variant, the vibrations were delivered to either the left or the right hand. In the spatial condition, stimuli alternated between the left and right side, while the temporal stimuli were always displayed on both sides at the same time. Spatial task stimuli were presented in a random combination of right and left side stimuli in two sequences of six stimuli, with 100-ms gaps between each presentation.

In the task conditions, participants had to decide whether the two sequences in a pair were the same or different; they indicated their choice by pressing one of two response buttons. In the no-task control condition, sequences were regular and always the same (Fig. 2A). Temporally regular sequences consisted of stimuli displayed for the same period of time (125 ms), while spatially regular sequences consisted of stimuli displayed in turn on the left and right sides of the screen

Table 1. Deaf and hard of hearing participants

General			Deafness			Hearing aids / cochlear implants				
1	2	3	4	5	6	7	8	9	10	11
	Age	Sex	Level of deafness	Diagnosis	Cause of deafness	Did you ever use hearing aids in the past?	Are you using hearing aids now?	How well do you understand speech when using hearing aids?	How well are you able to understand speech without seeing the person talking?	Cochlear implant
1	37	F	90 dB	Profound deafness	Medical mistake	Yes	Yes	Well	Poor	No
2	30	F	90–119 dB	Profound deafness	Unknown	Yes	Yes	Moderate	No	No
3	19	F	90–119 dB	Profound deafness	Genetic defect	Yes	No	Moderate	No	No
4	26	F	90–119 dB	Profound deafness	Unknown	Yes	Yes	Moderate	No	No
5	41	M	> 120 dB	Absolute deafness	Unknown	No	No	–	No	No
6	26	M	90–119 dB	Profound deafness	Genetic defect	Yes	No	Poor	No	No
7	42	F	90–119 dB	Profound deafness	Unknown	Yes	Yes	Poor	No	No
8	25	F	90–119 dB	Profound deafness	Unknown	Yes	No	Well	Poor	No
9	24	M	> 120 dB	Absolute deafness	Genetic defect	No	No	–	No	No
10	35	F	115 dB	Profound deafness	Genetic defect	Yes	Yes	Poor	No	No
11	30	M	90–119 dB	Profound deafness	Unknown	Yes	Yes	Poor	Moderate	No
12	21	M	90–119 dB	Profound deafness	Unknown	Yes	Yes	Well	Moderate	No
13	23	M	90–119 dB	Profound deafness	Unknown	Yes	No	Well	No	No
14	21	F	100 dB	Profound deafness	Unknown	Yes	Yes	Well	Poor	No
15	34	M	> 120 dB	Absolute deafness	Genetic defect	No	No	–	No	No
16	23	M	85–90 dB	Profound deafness	Genetic defect	Yes	No	Well	Well	No
17	23	F	90–119 dB	Profound deafness	Genetic defect	Yes	No	Moderate	No	No
18	31	F	90–119 dB	Profound deafness	Genetic defect	Yes	No	Well	Poor	No
19	40	F	90–119 dB	Profound deafness	Unknown	Yes	Yes	Poor	No	No
20	34	F	90–119 dB	Profound deafness	Genetic defect	No	No	–	No	No
21	29	M	90–119 dB	Profound deafness	Genetic defect	Yes	Yes	Poor	No	No

Options for question 9: poor, moderate, good, very good. For question 10: not at all, poor, moderate, good, very good. Scale of possible answers for question 12: none, poor, moderate, good, fluent. For questions 13 and 15: never, rarely, sometimes, often, all the time.

Table 2. Deaf and hard of hearing participants

Language		12	13	14	15	16	17	18	19	20
lp.	How well do you know PJM?	How often did you use PJM in your childhood?	In your childhood, did you speak in PJM with deaf adults?	How often do you use PJM now?	What is your main way of communicating now?	Is your mother deaf?	Is your father deaf?	From whom did you learn PJM?	Since when have you used PJM?	
1	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
2	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since elementary school	
3	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
4	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
5	Fluent	Often	Yes	Often	PJM	Yes	Yes	Parents	Always	
6	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since school	
7	Well	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
8	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
9	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
10	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
11	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
12	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
13	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
14	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since school	
15	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
16	Fluent	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
17	Well	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
18	Moderate	Often	Yes	Often	PJM	Yes	Yes	Teachers	Since primary school	
19	Moderate	All the time	Yes	All the time	PJM	No	No	Teachers	Since primary school	
20	Fluent	All the time	Yes	All the time	PJM	Yes	Yes	Parents	Always	
21	Fluent	All the time	Yes	All the time	PJM	No	No	Parents	Always	

Scale of possible answers for question 12: none, poor, moderate, good, fluent. For questions 13 and 15: never, rarely, sometimes, often, all the time.

(right/left hand). Subjects were asked to passively perceive the stimuli and then press a random button after their presentation.

Responses were given after each sequence pair within 2 s of the end of presentation. Subjects were presented with two visual and two tactile runs, the order of which was counterbalanced across subjects. In each of the four runs, subjects were presented with five blocks for each of the

eight conditions (temporal and spatial task in visual and tactile modalities; no-task in the visual and tactile modalities, see Fig. 1). Each experimental block comprised three pairs of sequences. Before each block, a visual cue that indicated the condition to follow was presented. Each presentation of a cue lasted 1 s and was followed by a gap of 1.5, 2.5, or 3.5 s, with a fixation point in the center of the screen. Blocks were separated

modality	VISUAL 				TACTILE 			
dimension	TEMPORAL 		SPATIAL 		TEMPORAL 		SPATIAL 	
task/ no task	TASK	NO TASK	TASK	NO TASK	TASK	NO TASK	TASK	NO TASK

Figure 1. Experimental design. The experimental design involved eight conditions: two sensory modalities, tactile and visual; two types of stimuli (dimensions), temporal and spatial; and two levels of task versus no-task (i.e., doing a task vs passive observation).

with rest periods of 8, 10, or 12 s. In both sensory modalities and all conditions, subjects were instructed to keep their eyes open and stare at the center of the screen. A training session in the visual and tactile modalities consisted of 20 trials for each task and familiarization with the passive observation condition. All tasks were presented using Psychopy3.

fMRI data acquisition

Data were acquired with a Siemens MAGNETOM Tim Trio 3T scanner using a 32-channel head coil. We used a gradient-echo planar imaging (EPI) sequence that is sensitive to blood oxygen level-dependent (BOLD) contrast (33 contiguous axial slices, phase encoding direction: posterior-anterior, 3.6-mm thickness, TR = 2190 ms, angle = 90°, TE = 30 ms, base resolution = 64, phase resolution = 200, matrix = 64 × 64). For anatomic reference and spatial normalization, T1-weighted images were acquired using a MPRAGE sequence (176 slices; FOV = 256; TR = 2530 ms; TE = 3.32 ms; voxel size = 1 × 1 × 1 mm).

Data analysis

All fMRI data were analyzed using the SPM12 software package (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). Data pre-processing included: (1) slice timing; (2) realignment of all EPI images to the first image; (3) co-registration of the anatomic image to the mean EPI image; (4) normalization of all images to MNI space; and (5) spatial smoothing (6-mm FWHM). All experimental conditions and six estimated movement parameters as regressors were first modeled within a general linear model for each participant.

Statistical analysis was performed on subject (first) and group (second) levels. On the first level, contrasts for all eight experimental conditions were computed: temporal and spatial task/control (no-task) conditions in both visual and tactile modalities. Then, to check for between group differences we computed main effect of group (deaf/hard of hearing vs hearing) and interaction effects of group and all three factors (task-no task, modality and dimension). For the significant main effects and interaction effects directional t-contrast were computed. Task-related responses were considered significant at a voxel-wise threshold $p < 0.05$, corrected for multiple comparisons across the whole brain using a voxel-level family wise error (FWE). To check for within-group effects in the auditory cortex of the deaf/hard of hearing, we also applied small-volume correction (SVC) with voxel-wise threshold $p < 0.005$, cluster-wise $p < 0.05$, corrected for multiple comparisons using FEW.

Two functionally guided region of interest (ROI) analyses were performed using MarsBaR 0.44 Toolbox. In the first analysis (see Functional ROI analysis), functional ROIs were defined as a 6-mm sphere centered around the peak of activation from the Bola et al. (2017) study (visual rhythms > visual control × deaf/hard of hearing > hearing subjects). Activation levels extracted from the ROI were then entered into an ANOVA with three within-subject factors (dimension: temporal/spatial, task vs no-task; modality: visual and spatial) and Bonferroni pairwise correction was performed to control for multiple comparisons.

In the second functionally guided individual ROI analysis, visual and tactile versions of the temporal task were used as independent localizers for each other. The right high-level auditory cortex mask was created using the *Neuromorphometrics* atlas in SPM12. From this region, we then extracted the 25 most significant functional voxels for the visual temporal sequences versus the temporal control contrast in the deaf/hard of hearing. These voxels were then used as an ROI for comparison between tactile tasks in the deaf/hard of hearing. Subsequently, the same procedure was applied to extract the 25 most significant voxels from the tactile temporal sequences versus the tactile temporal control condition contrast in the deaf/hard of hearing subjects within the right superior temporal gyrus. These voxels were then used as an ROI for comparison between visual conditions. In order to investigate the extent of the similarity between tactile and visually evoked activations, we applied this procedure to different ROI sizes consisting of the 10, 25, and 50 most significant voxels.

All behavioral analyses were performed using R Studio, version 3.0.1. Behavioral results obtained in the fMRI session for all four task conditions involving same/different decisions (temporal and spatial task in tactile and visual modality) were entered into a three-way ANOVA.

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Data availability statement

The datasets generated during the current study are available from the corresponding author on request and will be uploaded to NeuroVault (<https://neurovault.org/>).

Results

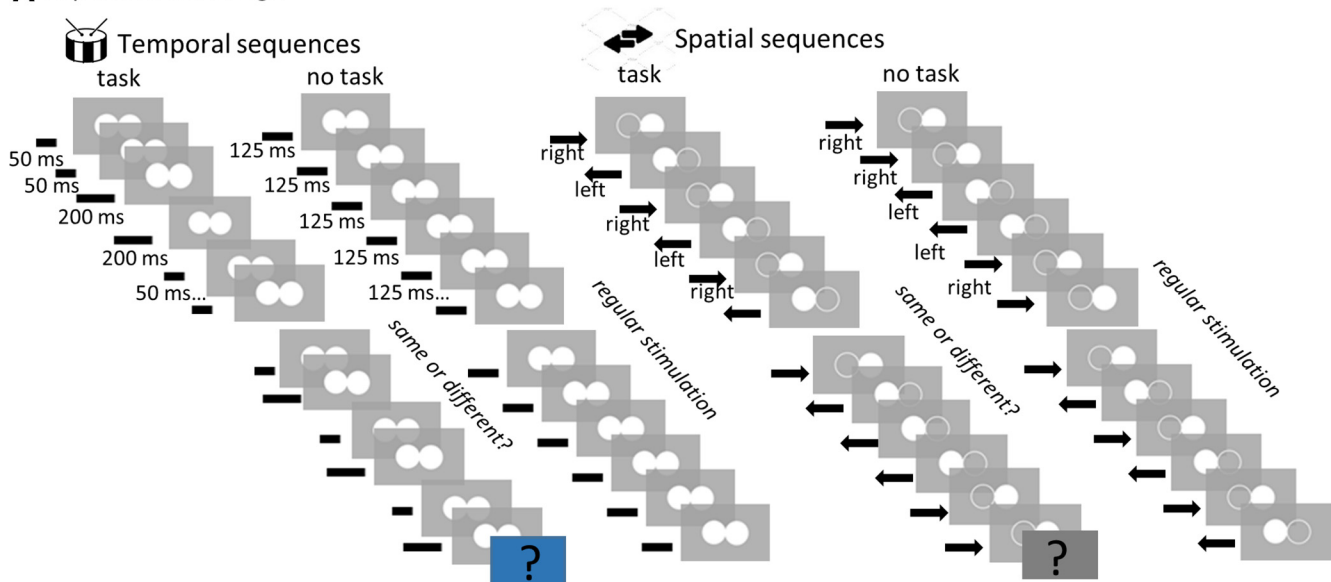
Behavioral results

Behavioral results (percentage of correct responses) are depicted in Figure 2B. Performance was above chance level in both deaf and hard of hearing ($t_{(41)} = 3.03$, $p < 0.01$) and hearing participants ($t_{(41)} = 14.48$, $p < 0.001$). Results were entered into a three-way ANOVA with two within-subject factors (dimension and modality), group as a between-subject factor, and with *post hoc* Bonferroni correction. We found a significant effect of group ($F_{(1,41)} = 10.41$, $p < 0.05$). Hearing subjects performed significantly better than deaf and hard of hearing subjects (hearing subjects: $M = 69\%$, $SD = 3.7$, deaf and hard of hearing subjects $M = 61\%$, $SD = 5.8$). No significant differences in performance level were found between the temporal and spatial discrimination tasks ($F_{(1,142)} = 2.25$, $p > 0.05$) or between the modalities ($F_{(1,142)} = 7.06$, $p > 0.05$). However, we found a significant effect of interaction of dimension and modality ($F_{(1,142)} = 10.02$, $p < 0.01$): the spatial task was significantly easier than the temporal task in the visual modality ($t_{(41)} = 3.23$, $p < 0.01$) but not in the tactile modality ($t_{(41)} = -1.03$, $p > 0.05$; Fig. 2B). We also found a significant effect of interaction between group and dimension ($F_{(1,142)} = 11.53$, $p < 0.01$): for deaf and hard of hearing participants, the spatial task was significantly easier than the temporal task ($t_{(41)} = 3.01$, $p < 0.01$), which was not the case in the hearing control group ($t_{(41)} = -1.36$, $p > 0.05$).

fMRI results

In line with the task-specific hypothesis, we anticipated that the effect of cross-modal reorganization within the auditory cortex should be consistent across different modalities but selective to one type of task (temporal). On the other hand, if the results showed that the right auditory cortex is activated for both the spatial and the temporal tasks, this would indicate that plasticity

A Experimental design



B Behavioral results

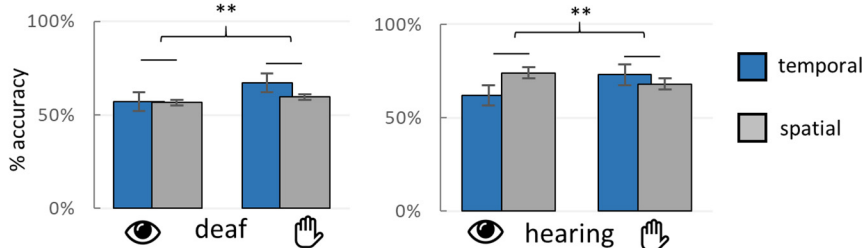


Figure 2. Experimental design and behavioral results. **A**, Experimental tasks. Temporal sequences: series of six flashes (white circles) presented on the screen, or a series of six tactile stimuli presented on four fingers of both hands for longer or shorter periods of time (50 or 200 ms with 100-ms blank interval between). The temporal sequences control condition involved presentation of a temporally regular series of stimuli (visual or tactile). Each stimulus was presented for the same duration (125 ms with a 100-ms blank interval between). **B**, Behavioral results. Performance in the fMRI (the accuracy of the same/different decision in the experimental task). Behavioral results were all significantly above chance level. There were significant differences between groups ($F = 12.57$, $p < 0.001$), but there were no significant differences between modalities or between types of task ($p > 0.05$). We found a significant effect of interaction of dimension and modality ($F_{(1,142)} = 10.02$, $p < 0.01$), and a significant effect of interaction between group and dimension ($F_{(1,142)} = 11.53$, $p < 0.01$); * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent SEM.

within the deprived auditory cortex may go beyond what is predicted by the task-specific hypothesis.

Whole-brain ANOVA

Our previous experiment (Bola et al., 2017) predicted that we would find differences limited to the posterior lateral right superior temporal gyrus. Nonetheless, before turning to examine these local differences, we first wanted to assess the entire extent of relevant brain activations. To this aim, we performed a whole-brain full factorial ANOVA analysis, where first-level contrasts were entered into a four-way ANOVA with group (deaf/hard of hearing vs hearing) as the between-subject factor and three within-subject factors: dimension (temporal/spatial), modality, and task versus no-task (Fig. 1).

In line with our hypothesis, the main effect of group revealed an activation cluster in the right auditory cortex, peaking in the superior temporal gyrus (MNI = 60, −20, 1, $F = 37.3$). Congruently with previous results, no such a significant effect has been found in the left hemisphere. An additional cluster of activation has been found in the supplementary motor area (MNI = −6, −2, 68, $F = 27.8$). Compared with hearing controls, deaf and hard of hearing subjects showed enhanced activity in the right auditory cortex especially in the right superior temporal

gyrus (deaf/hard of hearing > hearing, MNI = 60, −20, 1, $t = 6.11$, $p < 0.05$, voxel-wise FWE corrected). Other main effects which were not in the focus of this study are reported in the Table 3.

We then looked for whole-brain interaction effects of group with all three factors: dimension, task versus no-task, and modality. We found a significant cluster of activation for dimension × group in the right superior temporal gyrus (MNI = 66, −32, −12, $F = 38.7$). Interaction effect of the subject group and modality was not significant. When looking for simple effects which underlie this interaction, we found that spatial sequences evoked stronger activations than temporal sequences in deaf and hard of hearing participants (MNI = 66, −32, −12, $t = 6.32$; Fig. 3B).

Small-volume analysis, right superior temporal gyrus

We then focused our analysis on the central question of our study: the nature of the reorganization within the auditory cortex of deaf and hard of hearing individuals. Based on our previous experiment, we predicted that differences between conditions of interest in a group of deaf and hard of hearing subjects would be limited to the posterior lateral right superior temporal gyrus, which has previously been identified as a rhythm-related area (Bola et al., 2017). Based on this a priori hypothesis, we

Table 3. Whole-brain ANOVA main effects

Contrast	Region	Hemisphere	Cluster size	F value	MNI coordinates		
Main effect of modality (visual vs tactile)	Inferior occipital gyrus	Right	5653	408.86	30	−86	8
					18	−84	−10
					20	−94	4
	Inferior occipital gyrus	Left	4864	326.81	−16	−94	2
					−24	−88	6
					−18	−84	−12
	Central operculum	Right	371	56.60	48	−16	18
					52	−24	20
	Central operculum	Right	463	53.64	44	8	30
	Central operculum	Left	330	49.17	−56	−20	14
Main effect of task vs no task					−48	−24	20
	Superior frontal gyrus	Left	722	76.97	−22	−4	60
					−24	−6	52
					−36	0	58
	Middle frontal gyrus	Right	641	64.02	28	2	60
					26	−6	52
	Superior parietal lobule	Right	329	62.24	14	−68	58
	Superior parietal lobule	Right	366	54.93	38	−40	44
	Superior parietal lobule	Left	438	41.58	−32	−58	56
					−14	−70	52
Main effect of type of stimuli (temporal vs spatial)					−30	−50	42
	Supplementary motor area	Left/right	280	83.37	−4	0	62
					6	16	48
	Middle frontal gyrus	Left	2583	71.93	−28	24	54
					−18	56	32
					−36	20	50
	Precentral gyrus	Left	212	65.29	−46	−4	54
	Middle occipital gyrus		280	54.46	50	−68	24
					38	−80	26
	Angular gyrus	Left	1020	50.82	−48	−68	26
Main effect of group (deaf and hard of hearing vs hearing)					−42	−68	32
					−34	−74	46
	Posterior cingulate gyrus	Left	2171	50.40	−8	−46	36
					0	−44	36
	Middle frontal gyrus	Right	358	45.97	32	0	54
					52	6	46
					38.22	44	2
	Supramarginal gyrus	Right	290	42.73	46	−34	48
					48	10	24
	Fusiform gyrus	Left	200	37.62	−28	−42	−12
	Superior frontal gyrus		237	34.14	26	34	50
					18	46	44
					26	24	38
	Supplementary motor area	Left	6	27.86	−6	−2	68

employed an analysis with SVC, constrained by a 25-mm spherical ROI centered around the main effect reported in Bola et al. (2017)'s study ($p < 0.005$ voxel-wise, $p < 0.05$ cluster-wise, SVC FWE corrected).

Temporal processing in the visual and tactile modalities

We first asked whether the task-specific effect of the temporal sequences task that was revealed in the visual modality by our previous study would occur for both visual and tactile modalities. As Figure 4A shows, temporal sequences significantly activated the lateral right superior temporal gyrus when averaged over both modalities (temporal task condition relative to temporal no-task condition: temporal sequences > temporal control task

peak MNI = 58, −22, −4, $t = 5.43$). Moreover, while the activation induced by visual temporal stimuli was much stronger and more spread out across the auditory cortex than activation induced by tactile temporal stimuli, the activation for both modalities peaked in a very similar region (visual temporal task > no-task: tactile temporal task > no-task: MNI = 52, −18, −6, $t = 4.02$). The between-modalities overlap comprised an 87% tactile activation within the analyzed volume of the auditory cortex (Fig. 4B). A conjunction analysis revealed a significant cluster (visual temporal sequences and tactile temporal sequences, relative to no-task condition, conjunction) peaking in the superior temporal gyrus (MNI = 52, −18, −6, $t = 3.85$). Outcome of the analysis are reported in Table 4.

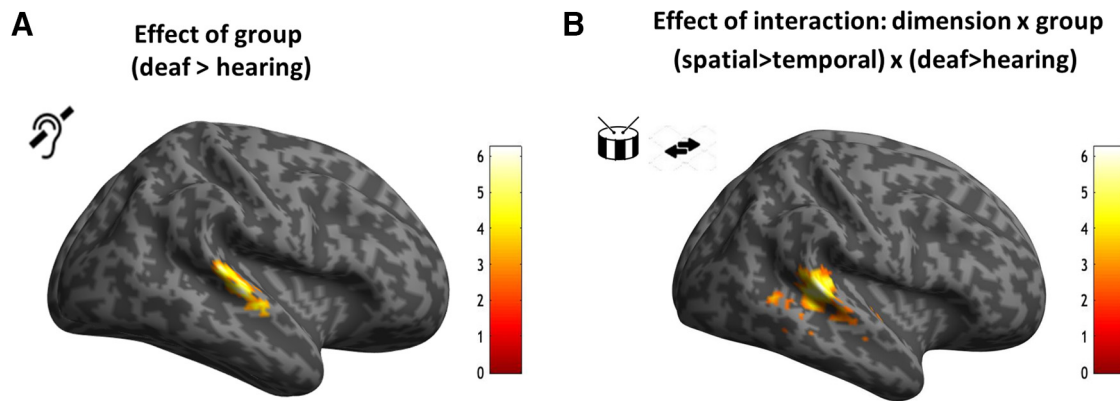


Figure 3. *A*, Visual and tactile processing lead to auditory cortex recruitment in the deaf and hard of hearing but not in the hearing. The effect of group (deaf/hard of hearing $\geq$ hearing) peaks in the right auditory cortex MNI = 60, -20 , 1 , $t = 6.11$. *B*, Interaction group $\times$ dimension in the right superior and middle temporal gyrus (MNI = 66, -32 , -12 , $t = 6.32$).

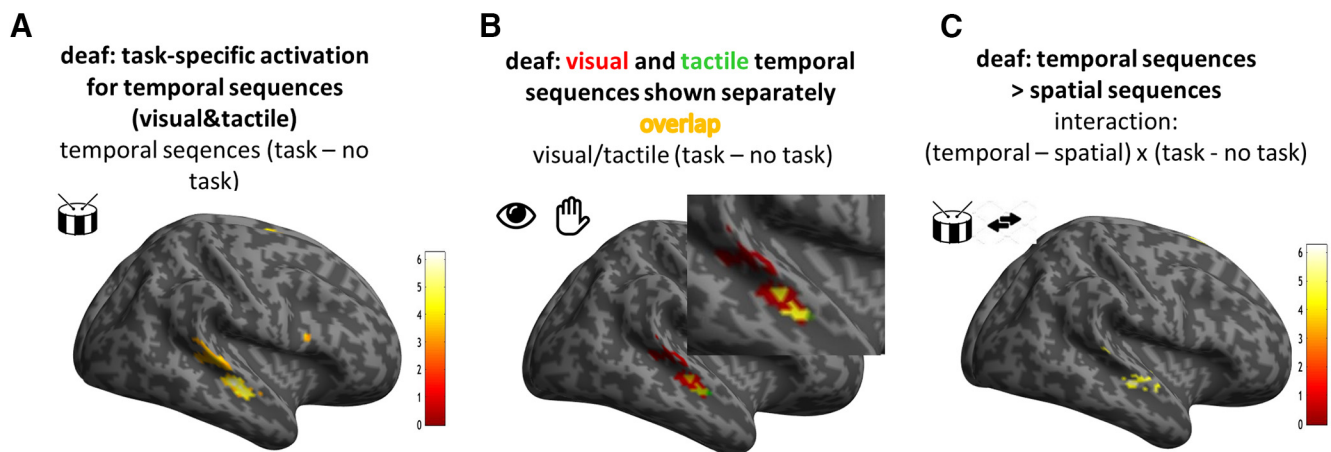


Figure 4. *A*, Task-specific effect for temporal stimuli (temporal sequences task $>$ temporal sequences no-task) for both modalities is reflected in an activation within the right auditory cortex MNI = 58, -22 , -4 , $t = 5.43$. *B*, Visual and tactile task activation peaks in a very similar region within the right auditory cortex. The overlap (yellow) between visual (red) and tactile (green) temporal sequences (for task–no-task condition) contains 87% of the tactile activation cluster. Temporal sequences and tactile temporal sequences (relative to no-task condition, conjunction) peaking in the superior temporal gyrus (MNI = 52, -18 , -6 , $t = 3.85$). Visually induced activation is more spread out across the auditory cortex than tactile activation. *C*, Comparison between temporal and spatial sequences discrimination task (relative to no-task) in both modalities revealed an activation cluster within right auditory cortex in deaf and hard of hearing subjects (temporal sequences $>$ spatial sequences $\times$ task $>$ no task) peak MNI = 60, -22 , 4 , $t = 4.18$. SVC analysis, threshold: $p < 0.05$, voxel-wise, FWE. All effects (*A–C*) were also equally significant as corrected within an alternative, anatomically defined ROI: the right superior temporal gyrus mask (neuromorphometrics); $p < 0.005$ voxel-wise, $p < 0.05$ cluster-wise, FWE corrected.

Temporal task versus spatial task

We then asked whether the reorganized auditory cortex is indeed selectively involved in temporal processing, or whether it acquires a more general function. According to our hypotheses, if the latter was the case, the auditory cortex in the deaf and hard of hearing should display either activity for other types of processing (spatial stimuli) or its activation should be related to a general attentional effort (task vs no-task) rather than to a specific task type.

In comparison to the control conditions in both cases, the selectivity of temporal processing should mean that auditory cortex activity is more intense for the temporal sequence discrimination task than for the spatial sequence discrimination task. This prediction was confirmed by the fact that a directional interaction analysis (temporal sequences $>$ spatial sequences $\times$ task $>$ no-task) revealed a cluster in the right STG (peak MNI = 60, -22 , 4 , $t = 4.18$; Fig. 4C). This suggests that cross-modal activation of the auditory cortex in the deaf and hard of hearing is at least partly specific for the temporal sequences discrimination task.

Given the heterogeneity of our subject group we cannot fully exclude the possibility that the main effects stated here are driven

by potential outliers in the subject group, specifically, by participants who may have access to the auditory experience when using hearing aids (hard of hearing individuals). In order to check for between-subjects consistency of the above-mentioned results, we performed a “leave-one-out analysis” on the group of deaf and hard of hearing individuals; 21-s level GLMs were performed, from each model one subject was left out. For each model we calculated the above-mentioned contrasts (as depicted in Fig. 4, temporal task $>$ no task, conjunction: temporal task $>$ no task: visual and tactile, interaction: temporal $>$ spatial $\times$ task $>$ no task). In all models and each contrast, we found a significant activation cluster within the right auditory cortex (at the threshold level $p < 0.001$, uncorrected). Thus, we conclude that the outcomes measured on the whole group are not disproportionately inflated by the outcome of any participant. Outcomes of the analysis are reported in Table 5.

Functional ROI analysis

To examine the relative direction and strength of the aforementioned activations and their spatial overlap, we employed a

Table 4. Small volume analysis

Contrast	Region	Hemisphere	<i>t</i> stat	Cluster size	MNI coordinates		
Whole-brain effects (between group) Effect of group: deaf (hard of hearing) > hearing	Superior temporal gyrus	Right	6.11	145	60	−20	2
					66	−30	10
Interaction: dimension × group Spatial > temporal × deaf > hearing	Superior temporal gyrus	Right	6.32	236	66	−31	12
					56	−38	10
Effects in the auditory cortex of the deaf and hard of hearing: temporal sequences (task > no-task, control)	Superior temporal gyrus	Right	5.43	456	58	−22	−4
					48	20	1
					64	−30	4
					60	−22	−4
Interaction effect of dimension (temporal > spatial) × (task > no-task)	Superior temporal gyrus	Right	4.18	210	66	−16	−8
					54	−12	6
					56	−20	−4
					−22	−6	60
Effect of task > no-task	Superior temporal gyrus	Right	3.52	129	56	−20	−4
	Superior frontal gyrus	Left	6.81	93	−24	−6	52
Whole-brain effects in the deaf and hard of hearing: effect of dimension (spatial > temporal sequences)	Superior frontal gyrus	Right	6.78	491	−36	−6	48
					26	−6	52
					32	2	50
					32	−2	48
	Middle temporal gyrus	Right	6.77	183	52	−54	6
	Superior parietal lobule	Right	6.21	285	34	−38	38
	Superior temporal gyrus	Right	5.51	171	63	−38	14
	Middle temporal gyrus	Left	5.42	145	54	−38	12

functionally guided ROI analysis. The ROI for this experiment was defined as a 6-mm sphere centered around the strongest peak of activation for visual rhythm processing in deaf subjects from our previous study (Bola et al., 2017; contrast: visual rhythms > control condition versus deaf/hard of hearing > hearing (MNI = 63, −16, −2; as described in Materials and Methods).

BOLD responses extracted from the ROI were entered into a within-subject ANOVA with three factors: modality (visual vs tactile), dimension (temporal sequences vs spatial sequences) and task versus no-task. The results replicated the effects found in the whole-brain analysis (Fig. 5A). In particular, they confirmed that the temporal discrimination task leads to significantly stronger auditory activation within the ROI than the spatial discrimination task when compared with the no-task condition (interaction of dimension × task vs no-task $F_{(1,142)} = 10.53$, $p = 0.014$; all results were corrected for multiple comparisons using the *post hoc* Bonferroni test; see Materials and Methods).

The analysis of simple effects confirmed that the level of task versus no-task was significant for temporal sequences ($F_{(1,142)} = 14.93$, $p < 0.001$) but was not significant for spatial sequences processing ($F_{(1,142)} = 0.012$, $p = 0.96$). This clearly confirms that cognitive engagement is crucial for auditory cortex recruitment, specifically for temporal processing. Consistent with previous analyses, we also found no significant main effect of modality ($F_{(1,142)} = 3.260$, $p = 0.225$), which suggests that visual and tactile processing similarly absorb neural resources in STG of deaf and hard of hearing subjects. Moreover, we found no significant interactions between the sensory modality and any other factor (spatial vs temporal and task vs no-task, all $p > 0.1$). Thus, not only the strength of auditory cortex involvement but also the activation pattern of different conditions and different levels of task versus no-task were similar for the tactile and visual modalities.

Our study revealed two important results: temporal task-specific activation and spatial activation overlap with each other in a particular part of the auditory cortex, defined on the basis of our a priori hypothesis. Together, these results confirm again that modality-independent activity of the auditory cortex depends on the behavioral task for temporal processing but remains independent of cognitive load for spatial sequence processing. Importantly, neither of these effects were significant for hearing subjects, for which the auditory cortex activation for each of the conditions was negligible (Fig. 5B).

Individual ROI analysis

Finally, since the outcomes of deprivation-driven plasticity might differ in subjects with various causes of deafness and various use of hearing aids, we performed an individual ROI analysis which takes into account anatomic and functional discrepancies between subjects. This analysis was conducted within the right superior temporal gyrus anatomic mask (see Materials and Methods; Fig. 6). We used individual peaks of activation from one modality (e.g., visual) to define individual ROIs for the analysis of activations from the other (e.g., tactile), and vice versa. The observations described in the previous sections of the paper were found to be largely independent of modality, i.e., they were found to be valid for both visual and tactile modalities. Here, we intend to verify this finding.

For each participant and each modality, we found a set of the 25 most active voxels within the superior temporal gyrus ($p < 0.05$, FWE corrected). In these individual ROIs, we tested the effects evoked by the other modality (see Materials and Methods).

Activation extracted from individual ROIs was entered into a three-way within-subject ANOVA with a *post hoc* Bonferroni test to adjust for multiple comparisons. The analysis revealed a significant effect of task versus no-task ($F_{(1,142)} = 8.8$, $p = 0.02$). The difference between auditory recruitment for the temporal

Table 5. Leave-one-out analysis, *t* values, and peak of activation for each of 21 GLM

Participant excluded from the analysis	Temporal task > no task (Fig. 4A)				Conjunction: visual and tactile temporal task > no task (Fig. 4B)				Interaction: temporal > spatial × task > no task (Fig. 4C)			
	<i>t</i> value	Peak MNI coordinates			<i>t</i> value	Peak MNI coordinates			<i>t</i> value	Peak MNI coordinates		
		<i>x</i>	<i>y</i>	<i>z</i>		<i>x</i>	<i>y</i>	<i>z</i>		<i>x</i>	<i>y</i>	<i>z</i>
1	5.33	56	−20	−6	3.76	52	−18	−6	4.32	60	−22	−4
2	5.43	58	−22	−4	3.93	52	−18	−6	3.89	60	−22	−4
3	5.55	58	−22	−4	3.66	52	−18	−6	4.13	60	−22	−4
4	5.22	58	−22	−4	3.67	52	−18	−6	4.35	58	−22	−6
5	5.14	56	−20	−6	3.71	52	−18	−6	4.23	60	−22	−4
6	5.34	56	−20	−6	3.8	52	−18	−6	3.88	60	−22	−4
7	5.72	58	−22	−4	3.9	52	−18	−6	3.88	60	−22	−4
8	5.47	56	−20	−6	4.15	52	−18	−6	4.05	60	−22	−4
9	5.32	56	−20	−6	3.79	52	−18	−6	3.95	60	−22	−4
10	5.29	58	−22	−4	3.57	52	−18	−6	4.37	60	−22	−4
11	5.05	56	−20	−6	3.48	52	−18	−6	4.3	60	−22	−4
12	5.37	56	−20	−6	4.09	54	−16	−4	4.04	60	−22	−4
13	5.07	56	−20	−6	3.65	52	−18	−6	4.39	58	−22	−6
14	5.18	56	−20	−6	3.76	54	−16	−4	4.28	60	−22	−4
15	5.19	58	−22	−4	3.74	52	−18	−6	4.2	60	−22	−4
16	5.42	58	−22	−4	3.84	52	−18	−6	4.15	58	−22	−6
17	5.21	58	−22	−4	3.52	52	−18	−6	4.18	58	−22	−6
18	5.48	58	−22	−4	3.92	54	−16	−4	4.07	60	−22	−4
19	5.44	58	−22	−4	3.83	52	−18	−6	3.6	60	−22	−4
20	5.75	56	−20	−6	3.71	52	−18	−6	4.19	60	−22	−4
21	5.64	56	−20	−6	4.09	52	−18	−6	4.1	60	−22	−4
Whole group analysis	5.43	58	−22	−4	3.85	52	−18	−6	4.18	60	−22	−4

From each of the linear models, one participant (from the group of deaf and hard of hearing individuals) has been left out.

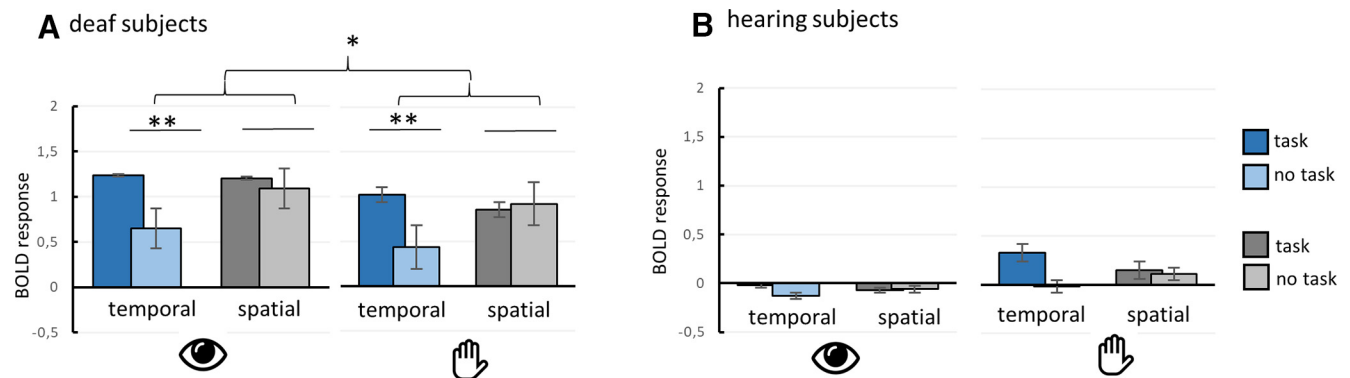


Figure 5. Results of the functional ROI analyses. The ROI was defined around the peak of activation (as revealed in the previous study) for the contrast: the visual rhythms condition versus the visual control condition. **A**, ROI analysis revealed a significant task-specific activation for temporal sequences versus temporal control condition in both the visual and tactile modalities. This effect is specific for the temporal task but not for the spatial task. The analysis revealed a significant effect of interaction: temporal sequences relative to spatial sequences (task vs no-task). **B**, No significant activation within the ROI in the hearing subjects. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent SEM.

and spatial tasks relative to passive observation was marginally significant (interaction of dimension: spatial vs temporal with task vs no-task, $F_{(1,142)} = 5.53$, $p = 0.043$). When we analyzed each dimension (spatial and temporal) independently, we again found that the task versus no-task factor is highly significant for temporal processing ($F_{(1,142)} = 13.5$, $p < 0.001$) but is not significant for spatial processing ($F_{(1,142)} = 0.53$, $p = 0.26$). Finally, we confirmed that activations within individual ROIs do not differ across modalities (main effect of modality: $F_{(1,142)} = 0.158$, $p = 0.692$). Additionally, we compared these results across different ROI sizes (10, 25 and 50 most significant voxels within the mask) to find the extent of similarities between modalities. We performed an additional ANOVA with ROI size, task versus no-task, dimension and modality as within-subject factors. We

found no significant main effect of size (main effect of size $F_{(2,142)} = 0.08$, $p = 0.77$) and no significant interactions between ROI size and any other factor (modality, task vs no-task or dimension, all $p > 0.1$).

These results confirm that a similar region is activated for both tactile and visual sequences; the pattern of task-specific effects remains the same for both modalities, although the recruitment of the auditory cortex is generally stronger for visual stimulation.

Discussion

The purpose of our study was to investigate task-specific auditory cortex activity in the reorganized brain. We wanted to verify

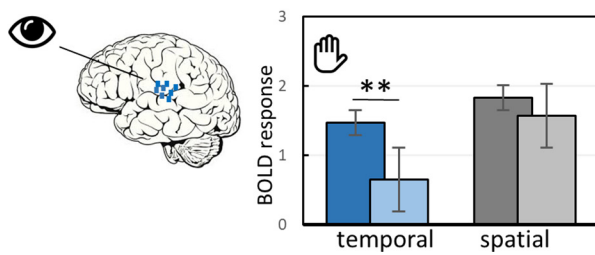
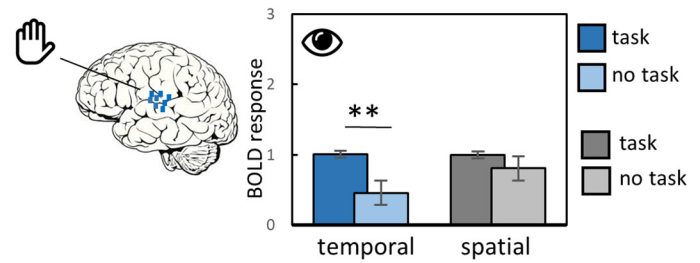
A Visual temporal sequences**B Tactile temporal sequences**

Figure 6. Results of the ROI analysis in which activations in the auditory cortex induced by visual temporal sequences (visual rhythms) and tactile temporal sequences were used as independent localizers for each other. **A**, ROIs for comparison between visual conditions were defined based on tactile temporal sequences versus regular visual stimulation (no-task) contrast. ROI analysis revealed a significant difference between the temporal visual sequence discrimination task and the temporal visual control condition. **B**, ROIs for comparison between tactile tasks were defined based on visual temporal sequences versus regular visual stimulation (no-task) contrast. ROI analysis revealed a significant difference between the temporal tactile sequence discrimination task and the temporal tactile control condition: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent SEM.

whether putative task-specific activations previously observed for temporal processing in the visual domain in deaf and hard of hearing participants also occur in the tactile modality. We also wanted to compare the processing of two different tasks (temporal vs spatial sequence discrimination) and question to what extent cross-modal auditory activations in deaf and hard of hearing subjects are actually task-selective. In line with our hypothesis, we showed that the effect of task-specific brain reorganization for temporal sequence discrimination that was previously demonstrated in the visual modality also occurs for tactile processing. Moreover, auditory cortex activation evoked by both visual and tactile stimuli occurred selectively for the temporal sequence discrimination task when compared with the spatial sequence discrimination task.

On the other hand, both the task and the control spatial conditions led to a strong activation of the right auditory cortex. As opposed to temporal condition activations, which appeared only when the subject performed a task, this spatial activation was present independently of whether a task was performed and could not be deemed task-selective. Overall, our results indicate that cross-modal auditory cortex recruitment in the deaf and hard of hearing is independent of modality (visual and tactile); however, in an unobvious way, it depends on the type of stimulation (temporal vs spatial).

Similar recruitment of the auditory cortex for tactile and visual stimuli in the deaf and hard of hearing

The main focus of previous studies of the auditory cortex of the deaf humans was on visual processing. Only a few studies demonstrated its role in tactile processing: in target detection (Auer et al., 2007), frequency discrimination (Levänen et al., 1998), and temporal and spatial discrimination (Bolognini et al., 2010). Experiments directly comparing cross-modal activations induced by visual and tactile tasks in the auditory cortices of the deaf individuals have been limited to studies on deaf cats. These show that stimulation in either the visual or tactile modality leads to recruitment of closely related regions (Lomber et al., 2011; Meredith and Lomber, 2011).

We showed that temporal sequence discrimination in both the visual and tactile modalities leads to a very similar activation pattern within the right auditory cortex. In a previous study, that part of the superior temporal gyrus was shown to be specifically recruited by visual rhythm processing in the deaf and by auditory rhythm processing in the hearing (Bola et al., 2017). Now, a direct comparison between a temporal task and a spatial task has revealed a task-specific activation within the same rhythm-

related auditory area in both visual and tactile modalities. This enhances our previous claim (Bola et al., 2017) concerning the task specificity of the auditory cortex of the deaf.

Since all our deaf and hard of hearing participants are proficient signers, we cannot exclude the possibility that some of the cross-modal effects that were observed resulted from language acquisition and not sensory deprivation (Bavelier et al., 2001; Cardin et al., 2013, 2016). However, the activation patterns evoked by visual and tactile stimuli were very similar, and tactile perception, unlike visual processing, does not seem to be directly connected with sign-language acquisition. This constitutes an argument for sensory-driven but not language-driven task-specific reorganization.

Our spatial stimulus was a series of right-left flashes appearing at regular intervals and thus incorporated temporal aspects. The partial similarity of the temporal/spatial stimuli might explain why we failed to find areas with a preference for the tactile task over the spatial task. However, this temporal aspect of spatial stimuli is roughly equal to the analogous aspect of the temporal control stimulus, yet the latter did not elicit automatic auditory cortex activations. Something in our spatial stimulus other than its temporal structure must have been driving activation, even in the absence of a task.

Different patterns of auditory cortex recruitment for spatial/temporal tasks

Temporal sequence processing led to auditory cortex recruitment for the task-involved condition but not for the task-free control. On the other hand, the spatial sequences elicited enhanced auditory cortex activations, regardless of any task. We must conclude that the revealed cross-modal effects are neither simply attention-driven nor selectively evoked by a specific task. They could be explained by an interplay between task-specific and more general effects. They could result from two separate phenomena operating in the reorganized auditory cortex that are related to the two different stimulus types. Alternatively, they could be attributed to a common general mechanism of sensory-driven attention which is merely differently triggered by temporal and spatial stimuli.

Temporal and spatial processing as separate phenomena

Although both temporal sequences and spatial sequences led to significant activation within the “rhythm-related” area identified in our previous study (Fig. 5A), spatial stimulus-driven activation is much more dispersed within the auditory cortex (Fig. 4C).

This may suggest that responses to the two types of stimuli (temporal and spatial) reveal two different phenomena. The auditory system has an advantage over the visual and tactile systems in the processing of temporal stimulation (Grahn, 2012; Cameron and Grahn, 2014). Arguably, because the deaf individuals do not experience the rich temporal content of the auditory stimuli, they exhibit lower accuracy in perception of visual temporal durations (second range) and in perception of tactile temporal durations (millisecond range; Bolognini et al., 2012).

However, the need for additional compensatory neural resources cannot explain task-independent auditory cortex recruitment for spatial sequences. Instead, one might interpret this effect in the light of several articles that report visual motion-driven plasticity in congenitally deaf humans (Bottari et al., 2011; Scott et al., 2014; Benetti et al., 2021). The stimulus used in the spatial condition moves from the right to the left side of the para-foveal visual field, or from the right to the left hand in the tactile condition; as such, it can be considered a motion-related stimulus. There is prominent evidence showing that moving stimuli can evoke auditory cortex activation in deaf humans. These cross-modal effects are reflected in behavioral enhancement in the domain of motion processing (Scott et al., 2014). The spatial stimulus used in our study may automatically engage the auditory cortex in the deaf and hard of hearing because of its motion-related properties. On this basis, it is possible to differentiate between task-driven, compensatory auditory activation for the temporal task, and automatic, bottom up, task-unspecific auditory cortex recruitment for the spatial task.

Temporal and spatial processing as one common phenomenon

An alternative explanation would be to attribute both spatially and temporally evoked cross-modal effects to one common mechanism of automatic, unintentional attention capture that is operating for both temporal and spatial stimuli.

Temporal and spatial sensory processing in deafness are similar in terms of neural correlates within the auditory cortex in the deaf humans. Performance in temporal and spatial tactile discrimination tasks in the deaf is equally disrupted by Transcranial Magnetic Stimulation delivered to the auditory cortex (Bolognini et al., 2010). The auditory cortex of the deaf individuals is causally involved in both temporal and spatial processing, at least in the tactile modality. Our results revealed a similar auditory activation strength for both types of stimuli within the ROIs (Figs. 5, 6). The cross-modal effects revealed in our study did not simply depend on performing a task, and they cannot be simply attributed to goal-directed attention itself. They could, however, be explained by automatic attention capture.

Several studies on the deaf suggested that they differ from the hearing in aspects of visual attention (Bavelier et al., 2000; Dye and Bavelier, 2013; Dye and Hauser, 2014). It has been shown that the auditory cortex in the deaf may be involved in attention-related processing, especially attention-shifting between central and peripheral vision. Recent studies have revealed that the auditory cortex in deaf individuals is recruited for switching tasks and the visual change task (Bottari et al., 2014), which also requires reorientation of attention from one stimuli or one part of visual field to another.

Recruitment of the auditory cortex in the deaf and hard of hearing in response to visual and tactile stimuli may be explained by similar processes of automatic attention. In our study, spatial stimuli, unlike temporal sequences, could attract attention automatically, independently of whether any task is performed. In turn, temporal sequences would attract attention only when they

are irregular and temporally complex, which is the case with the task-related condition but not the control condition. Only the latter would be salient enough to attract attention.

Several studies show that moving stimuli capture more attention than static ones (Abrams and Christ, 2003), and a changing or alternating (for example from left to right) stimulation captures more attention than non-changing stimulation (Franconeri and Simons, 2005). Visually evoked auditory cortex recruitment for moving stimuli and temporally complex sequences could be related to attention capture. According to this view, whether or not the auditory cortex is involved in sensory processing in the deaf and hard of hearing would depend on how salient stimuli are rather than how specific a task is.

In conclusion, overall, our results revealed task-specific auditory cortex recruitment for temporal sequences and strong unspecific auditory recruitment for spatial sequences. Both effects were independent of modality, thus demonstrating that the reorganized cortex in the deaf and hard of hearing becomes engaged in both visual and somatosensory processing. These effects imply that auditory cortex cross-modal plasticity most likely cannot be fully explained by task specificity; nor can it be attributed simply to the acquisition of a specific higher cognitive function (e.g., attention). The observed differences in the processing of temporal and spatial sequences presumably result from an interplay of task-specific and pluripotent plasticity. Our results open several avenues for investigation of the full complexity of the cross-modal plasticity phenomenon.

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