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Decoding visual location from neural patterns in the auditory cortex of the congenitally deaf

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ABSTRACT

Sensory cortices of individuals who are congenitally deprived of a sense can undergo considerable plasticity and be recruited to process information from the senses that remain intact. Here we explore whether the auditory cortex of congenitally deaf individuals represents visual field location of a stimulus – a dimension that is represented in early visual areas. We used fMRI to measure neural activity in auditory and visual cortices of congenitally deaf and hearing humans while they observed stimuli typically used for mapping visual field preferences in visual cortex. We found that the location of a visual stimulus can be successfully decoded from the patterns of neural activity in auditory cortex of congenitally deaf but not hearing individuals. This is particularly true for locations within the horizontal plane, and within peripheral vision. These data show that the representations stored within neuroplastically-changed auditory cortex can align with dimensions that are typically of visual cortex.

Keywords: Neuroplasticity; Congenital deafness; Visual location; Sensory reorganization; fMRI; MVPA; Decoding

1. INTRODUCTION

Considerable plasticity can take place in individuals who are congenitally deprived of a sense. Work on congenital blindness has demonstrated remarkable changes both in neural processing and in cognitive performance for non-visual information. For instance, blind individuals show finer tactile and auditory pitch discrimination performance than sighted individuals (e.g., Gougoux *et al.*, 2004; Van Boven *et al.*, 2000). Moreover, putative visual occipital regions are recruited in blind individuals for non-visual processing, such as braille reading (e.g., Sadato *et al.*, 1996).

Similar results have been obtained in congenitally deaf individuals. Studies with congenitally deaf non-human animals have shown extensive compensatory and cross-modal plasticity. For instance, the auditory cortex (AC) of congenitally deaf animals is co-opted to process visual (and somatosensory) stimuli (e.g., Hunt, Yamoah & Krubitzer, 2006; Kral, Schroder, Klinke, & Engel, 2003; Meredith & Lomber, 2011). In fact, some of these visually responsive neurons present characteristic response patterns typical of neurons within visual cortex (e.g., direction selectivity; e.g., Meredith & Lomber, 2011). Moreover, Lomber and colleagues (Lomber, Meredith & Kral, 2010; see also Meredith et al., 2011) showed that deaf cats are better than hearing cats in visual localization and motion detection tasks, and that these compensatory behaviors are dependent on certain structures of the AC.

Work on congenitally deaf humans has produced somewhat converging results, albeit much less conclusively. For instance, deaf individuals are better at detecting visual stimuli presented in the visual periphery (e.g., Neville & Lawson, 1987a; Reynolds, 1993), and discriminating and detecting visual motion than hearing individuals (e.g., Bavelier *et al.*, 2000; Bosworth & Dobkins, 2002; Neville & Lawson, 1987a). These individuals also demonstrate heightened tactile sensitivity (Levanen & Hamdorf, 2001). Correspondingly, putative AC in congenitally deaf individuals can be responsive to non-auditory stimulation – Finney and colleagues showed that the AC of congenitally deaf, but not of hearing participants, responds to simple visual stimulation (e.g., Finney, Fine & Dobkins, 2001; see also Karns, Dow & Neville, 2012; Levanen, Jousmaki & Hari, 1998; Nishimura, *et al*., 1999; Scott *et al.,* 2014; but see Hickok *et al*., 1997).

The fact that non-typical sensory information is processed in deafferented sensory regions (e.g., visual information in putative AC of deaf individuals) raises questions about the type of information represented in these cortices: what is being represented in the neuroplastically changed auditory cortex of congenitally deaf humans? A visual property that is central to visual processing in visual cortex is visual field location (e.g., Sereno et *al*., 1995). Hence, if AC of congenitally deaf individuals contains representations of particular visual properties, one likely candidate would be visual field location. Here we test congenitally deaf and hearing individuals in a visual task using fMRI to address whether human AC represents the location of a visual stimulus.

2. MATERIALS AND METHODS

We use functional magnetic resonance imaging (fMRI) and present stimuli typically used to map visual field preferences in early visual cortex (Zhang, Zhaoping, Zhou & Fang, 2012; see also Sereno *et al.*, 1995). We analyze patterns of BOLD response in auditory and visual cortex of 10 congenitally deaf and 10 hearing individuals using between-subject multivariate pattern analysis (MVPA; e.g., Haxby *et al.*, 2001, 2011). The focus of this experiment is on understanding whether the AC of deaf individuals is capable of representing visual information about a stimulus location in the visual field.

2.1 Participants. Sixteen hearing individuals and fifteen congenitally deaf naïve individuals participated in the Experiment. All participants had normal or corrected-to-normal vision, had no history of neurological disorder, and gave written informed consent in accordance with the institutional review board of Beijing Normal University (BNU) Imaging Center for Brain Research. All congenitally deaf participants were proficient in Chinese sign language, had hearing loss above 90 dB binaurally (frequencies tested ranged from 125 to 8000 hz), and did not benefit from the use of hearing aids. All hearing participants reported no hearing impairment or knowledge of Chinese sign language. The full data sets from five deaf and six hearing participants was discarded because of excessive head motion (above 3 mm during any of the sessions) or because of low fMRI signal-to-noise ratio (based on the variance of the standardized average values of the whole brain signal for each time point).

Participants in the hearing group were between the age of 18 and 22 (mean age=20.1 years) and included 3 males; participants in the congenitally deaf group were between 17 and 22 (mean age=20.4 years) and included 2 males.

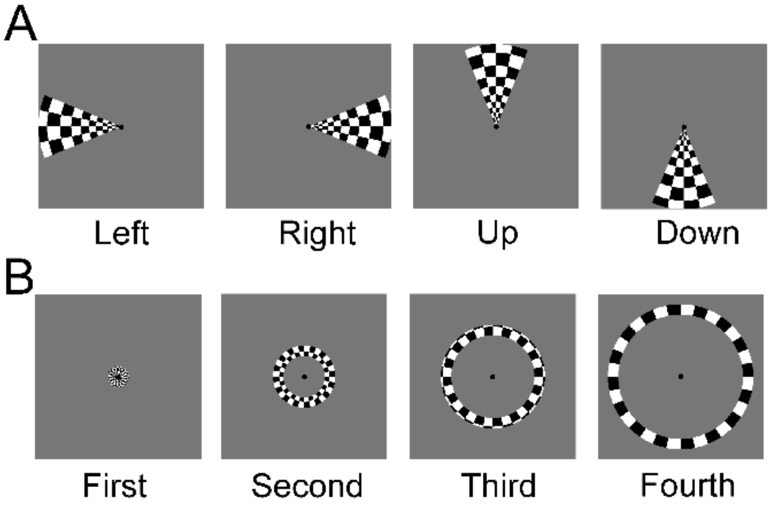


Figure 1. Stimuli used in the experiments. (**A**) stimuli used for visual field location classification; and (**B**) stimuli used for eccentricity classification.

2.2 Stimuli and procedure. Participants viewed two types of visual stimuli that were used to calculate visual-field maps (rotating wedges and expanding annuli; Zhang et *al.*, 2012; see also Sereno *et al.*, 1995). The first type were counterphase flickering (5 Hz) checkerboard wedges of 10.50° located at the (left or right) azimuth and (up or down) meridian planes (see Figure 1A). The second type of stimuli were counterphase flickering (5 Hz) checkerboard annuli of 9.23°, 6.61°, 3,97°, or 1.30° (see Figure 1B). Participants completed 4 runs: two that randomly alternated the wedge stimuli and two that randomly alternated the annuli stimuli. In each run, stimuli were presented in 12-s blocks with 5 repetitions of each stimulus per run. The stimuli were presented consecutively without any rest period in between.

2.3 Analysis.

2.3.1 MRI acquisition. MR data were collected at the BNU MRI center on a 3T Siemens Tim Trio scanner. Before collecting functional data, a high-resolution 3D structural data set was acquired with a 3D-MPRAGE sequence in the sagittal plane (TR: 2530 ms, TE: 3.39 ms, flip angle: 7 degree, matrix size: 256 × 256, voxel size: 1.33 × 1 × 1.33 mm, 144 slices, acquisition time: 8.07 min). An EPI sequence was used to collect functional data (TR: 2000 ms, TE: 30 ms, flip angle: 90, matrix size: 64×64, voxel size: 3.125 × 3.125 × 4 mm, 33 slices, inter-slice distance: 4.6 mm, slice orientation: axial).

2.3.2 Functional MRI data preprocessing. All MR data were analyzed using Brain Voyager QX. The anatomical volumes were transformed into a brain space that was common for all subjects (Talairach & Tournoux, 1988). Preprocessing of the functional data included slice scan time correction, 3D motion correction, linear trend removal, and high-pass filtering (0.015 Hz; Smith *et al*., 1999).

2.3.3 Auditory localizer. In order to localize the AC, hearing participants went through a functional run where periods of white noise were interspaced with periods of silence. Each period lasted 12 seconds (white noise or silence), and the sequence of white noise and silence was repeated 10 times. Auditory cortex was defined as the area, in a group analysis, in normalized space, and on data from hearing participants, that responded more strongly to white noise than to no auditory tone (for a similar approach see Finney *et al*.,2001; Shiell, Champoux, & Zatorre, 2015).

2.3.4 Primary visual cortex (V1) localizer. V1 was defined from the analysis of the wedge stimuli, using a simplified version of the standard phase-encoding method focusing on the vertical and horizontal meridians (Sereno *et al*., 1995; Zhang *et al*., 2012). As one moves from the middle of V1 to the V1/V2 border, the receptive field locations change from the horizontal to the vertical meridian. As one crosses the border from V1 and continues into V2, the receptive field locations move from the vertical meridian back towards the horizontal meridian. This reversal facilitates the definition of V1.

2.3.5 Between-subjects MVPA decoding analysis. We performed between-subject MVPA (Haxby et *al*., 2011) on beta values, having aligned all images anatomically in Talairach space (Talairach & Tournoux, 1988). The classification was performed with a SVM algorithm implemented with LIBSVM (Chang, C.C. and Lin, C.J., LIBSVM, a library for support vector machines, http://www.csie.ntu.edu.tw/~cjlin/libsvm/).

Annuli runs were analyzed separately from wedge runs. In both cases, we first run a general linear model (GLM) to estimate the magnitude of the response at each voxel for the 4 rings (or wedges) in each scan run. Specifically, each GLM consisted of 20 predictors (4 rings or wedges times 5 alternations) in which each stimulus presentation event was modeled as a unit impulse function convolved with a canonical hemodynamic response function. Beta values for each predictor in the model were extracted at each voxel. In total we had 40 beta values (20 predictors times 2 runs) at each voxel for each subject, 10 beta values for each ring (or wedge).

We then used multivoxel data from different subjects across the same or different experimental groups. As such, we have two types of classifiers: within-group and between-group classifiers. Within-group classifiers would be trained and tested with data from participants of the same group (e.g., deaf participants), whereas between-group classifiers would be trained on data from one group and tested on data from the other group. We trained the classifiers on data from 8 participants, and tested then on data from 2 other participants. Group membership of training and testing data sets would be dependent on the type of classifier (for an example see the Supplementary Material).

By using between-subject MVPA, and creating these two types of classifiers, we can more directly compare the two groups, and assess visual representational content in the AC of deaf and hearing adults. Classification was done over the four conditions of the wedge protocol, and over specific contrasts (left versus right; up versus down). We also tested classification over annuli stimuli, where we compared the inner-most rings (first and second rings) with the outer-most ring (i.e., center versus periphery classification).

Accuracy was computed as the averaged classification accuracy over all possible combinations, without repetition, of 2 participants whose data was used for testing the classifiers out of the set of 10 participants ($\binom{10}{2} = 10!/(2!\,8!)$; i.e., 45 data folds). Chance level was calculated over another set of MVPA computations performed with surrogate data. Surrogate data were constructed using original beta values of voxels in the same region-of-interest (ROI), but their labels were randomly shuffled (Watanabe *et al.*, 2011). Using surrogate data takes into consideration the intrinsic variability of our own data set, and as such, it may be a more natural way of assessing chance performance. Independent sample z-tests were performed over real and surrogate data and upper-bound confidence intervals were calculated and used as the threshold for chance level. We used the 99% confidence interval estimates as our canonical threshold to define above chance classification. We also calculated the 99.99% and 99.9999% confidence intervals for more stringent statistical comparisons.

2.3.6 Whole brain between-subjects searchlight MVPA. We performed whole-brain searchlight analysis (Kriegeskorte, Goebel & Bandettini, 2006) at the voxel level using in-house scripts under the same linear SVM algorithms used in the ROI analysis. This analysis was performed exclusively for the within-group conditions (i.e., training on deaf and testing on deaf, or training on hearing and testing on hearing) using the same cross validation procedures. The searchlight size was 33 voxels (i.e. voxels within 6 mm from the visited voxel were included). Statistical significance was assessed in a similar fashion as in the ROI analysis - we performed classifications on surrogate data over 180 iterations per voxel. As such, z maps are presented for the three classification conditions (left versus right; up versus down; and center versus periphery) for the two groups, and a z-value above 3.9 corresponds to a p-value equal to or less than 0.0001.

3. RESULTS

Representation of visual location in the AC of the Congenitally Deaf. In this experiment, we measured neural responses to counterphase flickering checkerboard wedges and annuli stimuli in visual and auditory cortices.

AC was defined as the region in hearing participants, and at the group level, that showed heightened responses to white noise compared to silence (*t* (1249) = 3.3, p<0.001, uncorrected; peak talairach coordinates in the right hemisphere x = 44, y = -19, z = 9; peak talairach coordinates in the left hemisphere x = -49, y = -19, z = 7; see Figure 2a and 2b). The peak talairach coordinates of our auditory region are within the 50-100% probability range of being in primary auditory cortex (Penhune, Zatorre, MacDonald & Evans, 1996; PAC – hA1 and hR; e.g, Da Costa *et al*., 2011). Moreover, as shown in Figure 2b, our region of interest clearly includes the Heschl's gyri, which is the principal anatomical landmark for PAC (e.g., Da Costa *et al*., 2011).

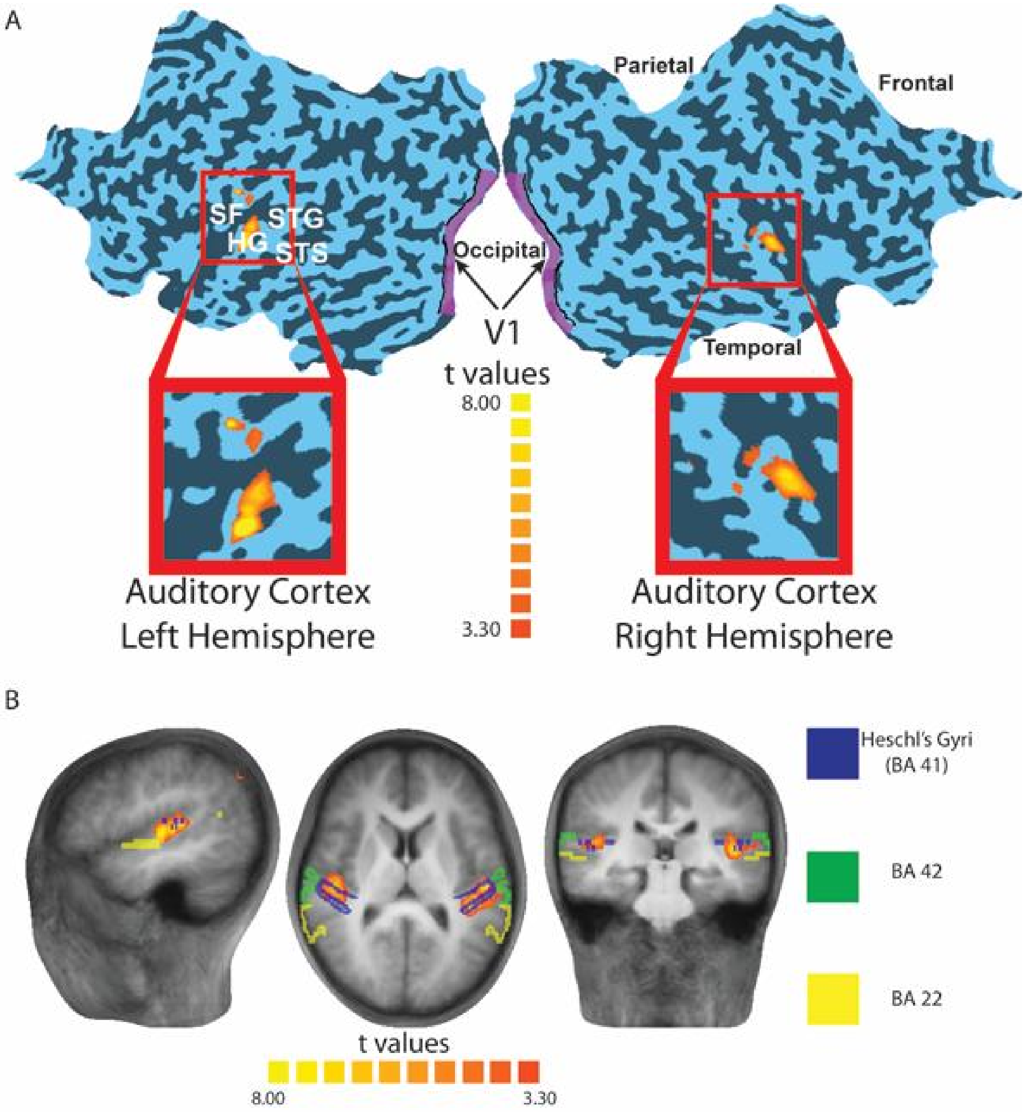


Figure 2. Auditory and visual cortex. (**A**) Regions within auditory cortex (AC), defined in hearing participants, and primary visual cortex used for the classification. (**B**) The auditory cortex ROI includes Heschl's Gyrus (Brodmann Area 41), but does not include other auditory regions of interest such as Brodmann Areas 42 and 22. *t* maps correspond to the AC ROI contrast of white noise vs. silence . HG – Heschl's Gyrus; SF – Sylvian Fissure; STG – Superior Temporal Gyrus; STS – Superior Temporal Sulcus.

However, there is a strong possibility that areas outside the PAC (e.g., belt regions of AC) are also part of our auditory ROI. The variability inherent in using group-level ROIs defined in a different group may undermine precise localization of PAC. Furthermore, it has been shown (Wong, Chabot, Kok & Lomber, 2013) that A1 of deaf cats suffers volumetric reduction and may be partially taken over by other neighboring areas, which would indicate that accurate localization of A1 in deaf individuals may be extremely hard. As such, we will loosely refer to our auditory region as the AC. This selected bilateral auditory region was used to test predictions in both the hearing and deaf groups.

We then used between-subject MVPA (e.g., Haxby *et al.*, 2001, 2011) to test whether AC in congenitally deaf individuals contains reliable information about the location of a visual stimulus (for univariate analysis see the Supplementary Material and Figure S1). Between-subject MVPA allows for a direct comparison between groups and thus tests how specific the results are for each group. We constructed “visual-field-location decoders” to classify neural activity in AC and V1 using linear support vector machine algorithms. The goal of classification was to decode the location within the visual field where the visual stimulus appeared (left/right/up/down) and its eccentricity (center/periphery). We employed multivoxel pattern classifiers with different combinations of learning and testing sets: within-group classifiers, trained on data from 8 participants from a group (i.e., deaf or hearing), and tested over data from the remaining 2 participants from that group; and between-group classifiers, trained on data from 8 participants from one group, and tested over data from 2 participants from the other group.

Critically, our results show that successful classification in AC is dependent on the learning/testing sets used for classification. Classifiers that learned from and/or were tested with input from hearing participants were not able to reliably decode the location of a visual stimulus (see Figure 3), indicating that activity in AC in hearing participants does not contain reliable information about where a stimulus was presented. The within-group classification in AC (bilaterally) of deaf individuals was, however, significantly better than chance (27.47%; upper-bound 99% confidence interval estimate for chance level: 26.82%; See Figure 3A). This above chance classification accuracy seems to be driven more by decoding of the azimuth/horizontal location (left vs. right) than the meridian/vertical location (up vs. down). Classification performance in AC for right/left classification was 57.61% (upper-bound 99,9999% confidence interval estimate for chance level: 57.24%) and 49.28% for up/down (upper-bound 99% confidence interval estimate for chance level: 54.22%; See Figure 3B). These above chance performances are only obtained for data from bilateral AC, and not for unilateral analysis for data from left or right AC.

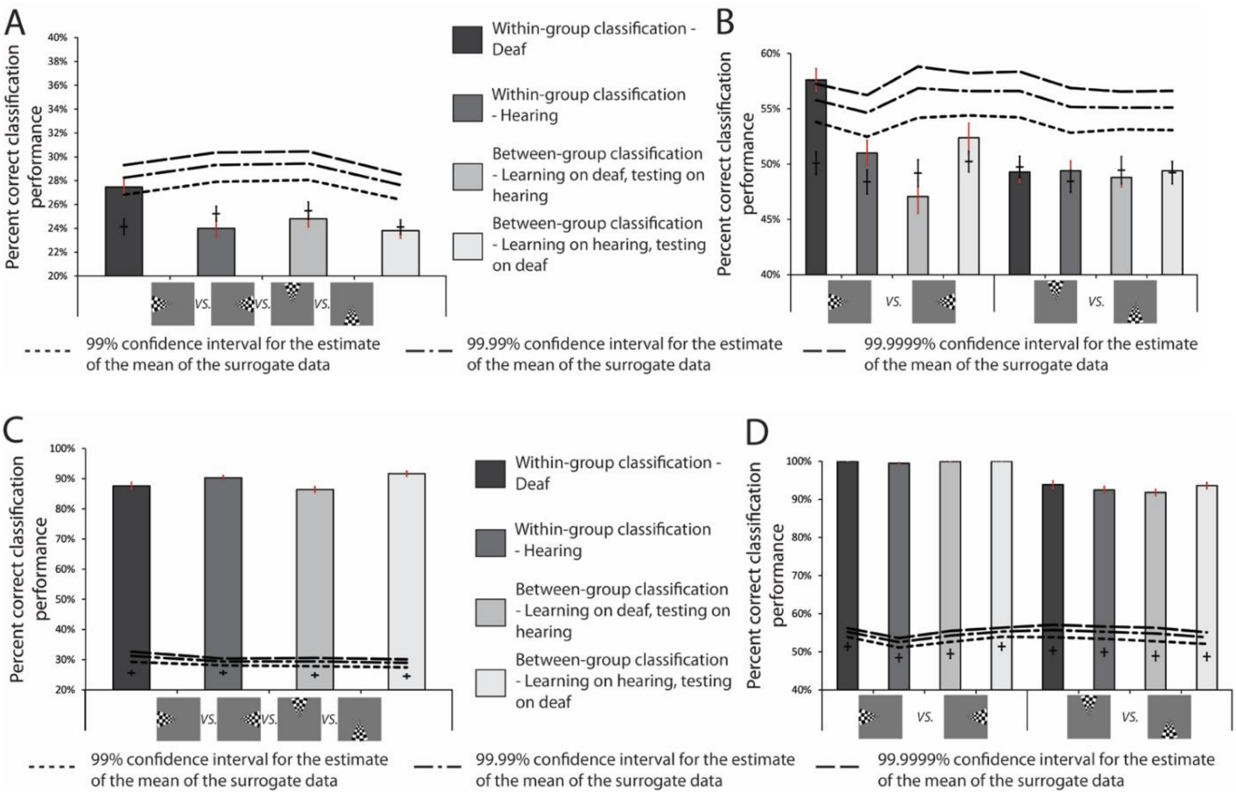


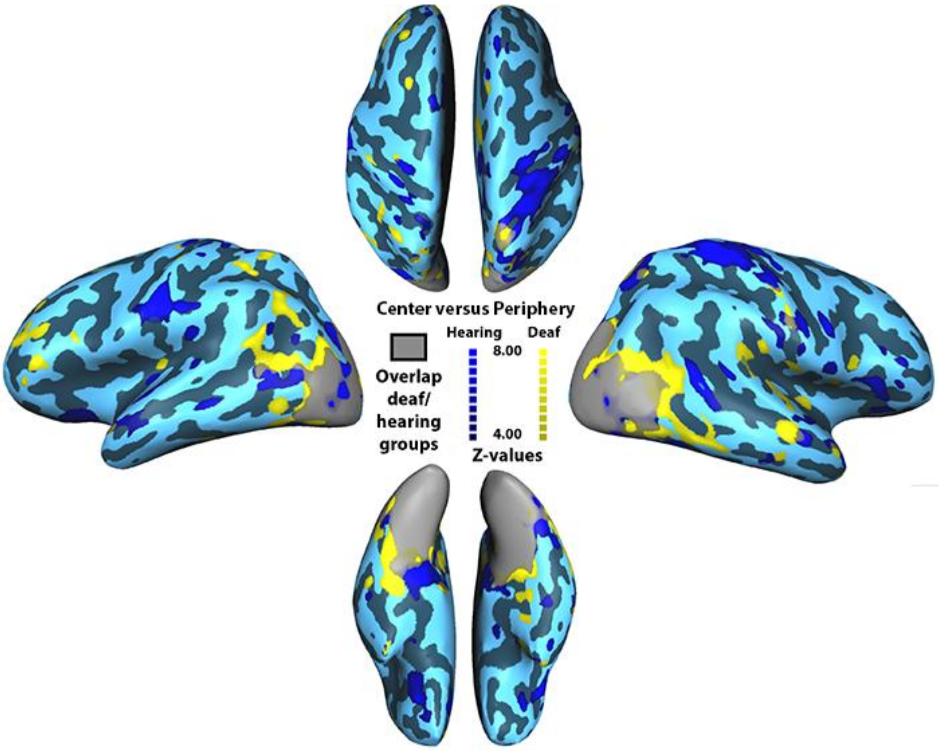
Figure 3. Percent correct performance for real and surrogate data in auditory cortex (bilaterally) and visual cortex. (**A**) Percent correct performance for quadrant classification in AC; and (**B**) Percent correct performance for the classification of the contrasts left vs. right and up vs. down in AC; (**C**) Percent correct performance for quadrant classification in V1; and (**D**) Percent correct performance for the classification of the contrasts left vs. right and up vs. down in V1. Bars correspond to performance with real data, and black dashes (-) correspond to performance with the surrogate data. Dashed lines correspond to different confidence intervals for the estimate of the mean of the surrogate data. Red error bars correspond to the SEM of the classification data, whereas black error bars correspond to the SEM of the surrogate data. Within-group classification performance for deaf individuals is above chance for quadrant classification, demonstrating that visual location is represented in the AC of congenitally deaf individuals. Stimuli along the azimuth, when compared to stimuli along the meridian plane, seem to drive responses in AC of congenitally deaf individuals. Results in V1 show highly significant classification performance across classifiers.

Finally, the within-group classification between the inner-most and outer-most locations of the stimulus in deaf individuals was also above chance for data from the right AC (and not for the left AC or bilateral AC; performance with data from right AC: 54.97%; upper-bound 99,999% confidence interval estimate for chance level: 54.96%). This means that beyond information on ‘quadrant’ location, the patterns of activity within AC of congenitally deaf individuals contain information about whether a stimulus was presented centrally or in the visual periphery. As expected, classification accuracies for neural patterns arising from V1 were near ceiling irrespective of the learning/testing set used (See Figure 3C and D for classification accuracy in V1).

Whole brain searchlight MVPA of visual field location in the Congenitally Deaf. We also performed a whole-brain searchlight analysis to identify other areas that contain information that could be used to decode locations within the azimuth (left vs. right) and the meridian plane (up vs. down), as well as between locations in the center and periphery of the visual field (see Figure 4), in both our deaf and hearing groups. In this analysis we have only tested within-group classification (e.g., training and testing on deaf participants).

Not surprisingly, classifying locations within the azimuth or meridian plane, or between central and peripheral positions could be performed within visual occipital cortex for both deaf and hearing individuals (Fig. 4). There were, however, other areas beyond occipital cortex where the location of a stimulus in the visual field could be successfully decoded. Decoding peripheral vs. central stimuli locations could be performed over data coming from superior parietal regions for both deaf and hearing participants, although this effect was more widespread for hearing than deaf participants. This classification was also reliably above chance in right superior and lateral temporal regions (e.g., around the AC) for deaf but not hearing participants (Fig. 4a). Decoding locations within the azimuth plane was possible within left parietal regions and right superior temporal and temporo-parietal regions (around the AC) for deaf individuals (Fig. 4b). In the hearing, decoding could be performed in bilateral anterior temporal regions, and in the right superior posterior temporal sulcus (Fig. 4b). Finally, it was possible to decode locations within the meridian plane in a more limited set of areas beyond occipital cortex and mainly for deaf individuals, in particular within bilateral temporal regions (Fig. 4c).

A.


Center versus Periphery
Overlap deaf/ hearing groups
Hearing
Deaf
8.00
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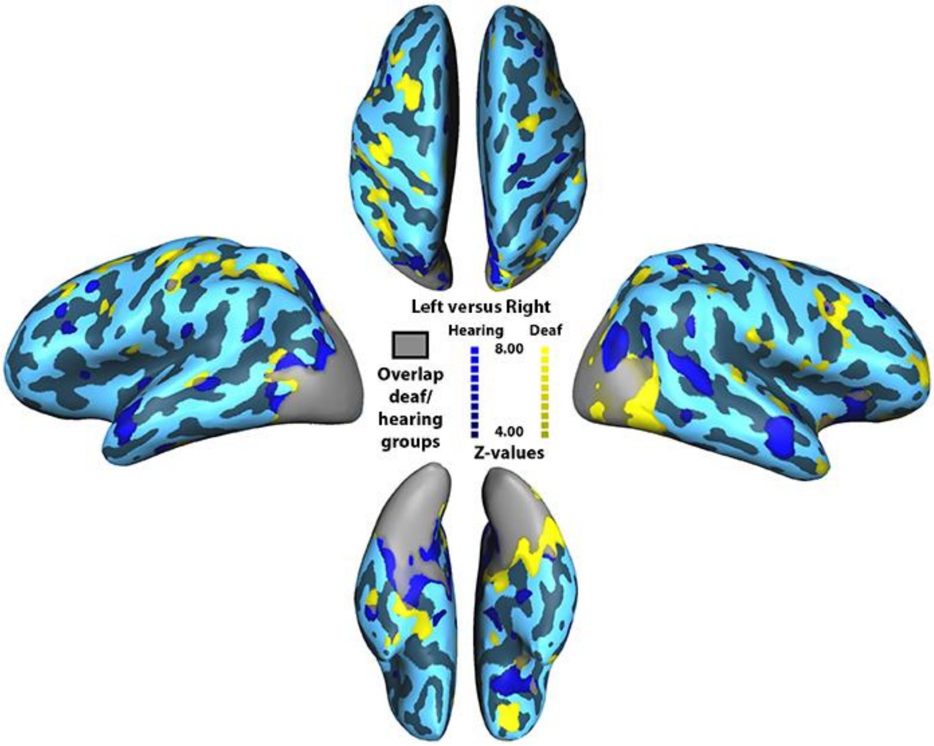
Z-values

B.


Left versus Right
Overlap deaf/ hearing groups
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Z-values

C.

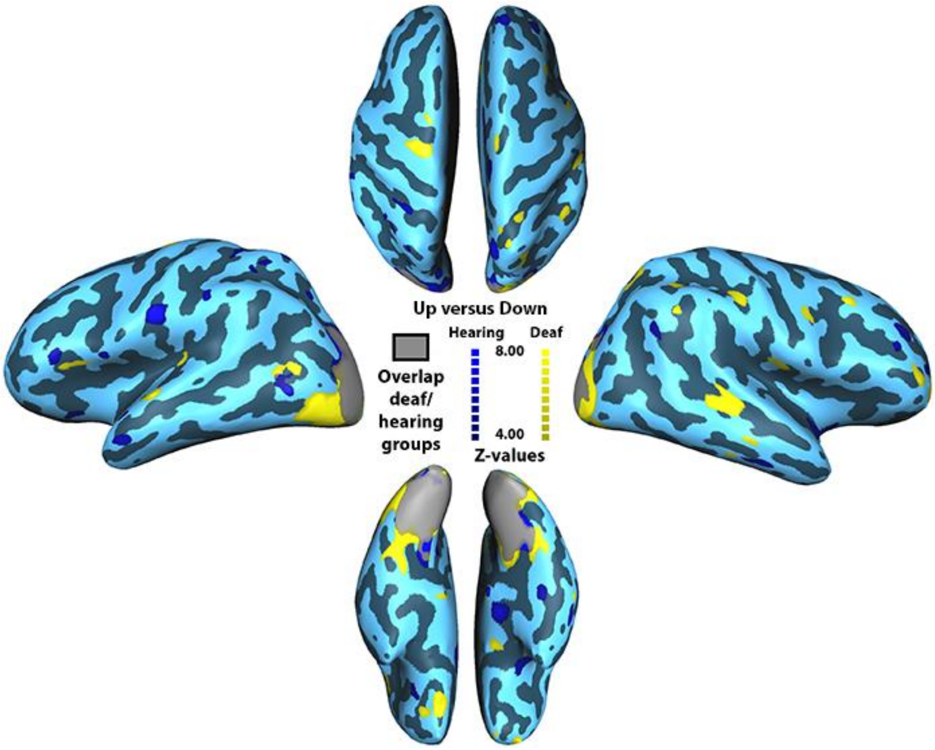

Figure 4. Whole-brain searchlight classification accuracy for center/periphery locations, and locations within the azimuth and meridian planes. (**A**) Activation maps (z-values) of performance for decoding center versus periphery locations across the whole-brain for deaf and hearing participants; (**B**) Activation maps (z-values) for performance decoding left versus right locations across the whole-brain for deaf and hearing participants; and (**C**) Activation maps (z-values) for performance decoding up versus down across the whole-brain for deaf and hearing participants. z-values (calculated against surrogate data) above 3.9 correspond to p-values equal to or less than 0.0001; Decoding performance for the deaf group is represented in yellow, whereas for the hearing group it is represented in blue. Overlap in decoding ability for both groups in represented in silver gray.

4. DISCUSSION

Here we show that the AC of congenitally deaf individuals contains reliable information about the location of a stimulus in the visual field. We found that the fMRI patterns in the AC (bilaterally) of congenitally deaf individuals can be used to decode the position of a stimulus, especially along the horizontal/azimuth plane. We were also able to decode from patterns of activation in the right AC of deaf individuals whether a stimulus was presented in central or peripheral vision. Moreover, whole-brain decoding results confirm the importance of temporal regions (mainly in the right hemisphere) for decoding peripheral and azimuth locations in the deaf. The implication of our results is that congenital deafferentiation of the AC leads to a remapping of visual information, and that along with this remapping, the content of the representations stored within the neuroplastically changed AC may follow dimensions that are typically seen in visual cortex. In particular, we show that one of the most ubiquitous visual properties – stimulus location in the visual field – can be decoded from the representations in the AC of congenitally deaf individuals.

Interestingly, the differential hemispheric contribution reported here for periphery versus center and left versus right may be suggestive of there being aspects of neuroplasticity specifically concerned with periphery vs. center, potentially associated with attentional processes, and which differentially depend on the right hemisphere, and aspects of neuroplasticity that focus on the azimuth dimension, and depend on the processing taking place within both hemispheres.

Whole brain searchlight analyses also suggested that multisensory and attentional networks (e.g., around superior parietal cortex) may be important for the representation of center/periphery locations in both hearing and deaf groups, and for the representation of the azimuth plane in deaf participants. This could be in line with the proposal that some of the neuroplastic effects within congenitally deaf individuals are due to a heightened ability to allocate attention to peripheral visual locations (e.g., Bavelier et al., 2000).

Our data are in line with those from research on visual responses within putative AC of deaf non-human mammals. The AC of these animals responds to visual and somatosensory information (e.g., Hunt *et al*., 2006; Kral *et al*., 2003; Meredith & Lomber, 2011). These cortices inherit properties typical of visual neurons. For instance, they seem to cover the contralateral visual field, and code for direction of motion and velocity (Meredith & Lomber, 2011). In fact, Roe, Sur and Colleagues (e.g., Roe *et al.*, 1990) showed that the AC of newborn ferrets in which the projections of retinal cells were surgically rerouted onto an auditory thalamic nucleus, show response patterns to visual stimulation similar to those observed in primary visual cortex. Most importantly, neurons within the AC seem to represent the visual field in a systematic way (Roe *et al*., 1990; but see Meredith & Lomber, 2011). Hence, the data herein regarding the representation of visual space in the human AC converge with extant animal data. Our findings raise the intriguing possibility that visual responses in the AC of the congenitally deaf could follow a systematic organization similar to what is observed within visual cortex (i.e., retinotopy). Evidence for such deep reorganization of the cortical surface under congenital sensory deprivation in humans has been demonstrated in blind individuals (Watkins *et al.*, 2014). Watkins and collaborators showed systematic representations of different sound frequencies within visual cortex. While no such evidence has been reported for the AC of the congenitally deaf humans, as described above, there is some evidence within the animal model for such organization (e.g., Roe *et al*., 1990). Regardless, it may nevertheless be the case that our findings are driven by a rudimentary type of organization in the AC of deaf individuals of visual stimulation along the azimuth plane. Thus, an important question to be addressed in subsequent studies is whether visual information in AC in deaf individuals follows a retinotopic organization.

Our data also suggest that the representations of the horizontal and vertical planes are not equivalently remapped in AC in deaf individuals. Here we showed a processing advantage for stimuli within the horizontal plane. Convergent results were obtained in studies with deaf cats and ferrets. Meredith & Lomber (2011) showed that the extended representation of the contralateral visual field observed in the anterior auditory field of deaf cats did not include the superior and inferior extremes of the visual field, whereas Roe *et al*. (1990) showed that the horizontal meridian is more precisely mapped than the vertical meridian in the AC of deaf ferrets.

Why should there be an advantage for the processing stimuli along the azimuth plane in congenital deafness? In order for the AC of deaf individuals to represent visual space, a two-dimensional spatial variable has to be coded instead of the typical one-dimensional sound variable (sound frequency). It is well known that certain areas of the AC (e.g., A1) are organized tonotopically, with an organization that follows an orderly preference for different frequencies (e.g., Da Costa *et al*., 2011). Within the bands that roughly show the same preference towards a particular frequency (isofrequency bands), other properties of sound are coded. Roe *et al*. (1990) suggested that because the pattern of projections from the auditory thalamus along the isofrequency axis is not as topographically organized as those along the tonotopic axis, and because, in their data, the vertical plane is represented along the same anterior-to-posterior dimension of cortex as the isofrequency axis, the orderly processing of visual stimuli within the vertical plane would not be fully feasible. An alternative possibility may be related to the fact that processing within the isofrequency bands codes for interaural differences – a cue for sound localization within the horizontal plane. Rajan, Aitkin & Irvine (1990) showed that there is a relative organization of responses to auditory stimuli by azimuth localization within the isofrequency bands of the AC of hearing cats. This organization could be the scaffolding for the enhanced processing within the horizontal plane.

Another interesting implication of our data is how the multisensory nature of the neocortex (Ghazanfar and Schroeder, 2006) can impact on neuroplasticity. It has been shown that stimuli presented in a particular modality (e.g., vision) that also implies some sensory experience in another modality (e.g., audition) can be meaningfully processed in the sensory cortices of both modalities, suggesting a high degree of multisensorial processing within primary sensory cortices. For instance, Meyer and colleagues (2010) presented three types of items (animals, musical instruments and man-made objects) visually in the absence of sounds. They were, however, depicted in a sound-implying fashion (e.g., a howling dog). They showed that those categories could be decoded from data from the AC. Vetter, Smith & Muckli (2014) showed that information within the visual cortex of blindfolded individuals can be used to decode complex stimuli (birds, traffic and people) conveyed by auditory input. Our stimuli do not have a multisensory property, and as such may not be amenable to show these multisensory effects in normal participants. Nevertheless, the intrinsic multisensory nature of the sensory cortices may be what the system exploits under sensorial deprivation, thus facilitating the emergence of the neuroplastic changes presented here.

An important question for our understanding of the results of our experiment is related to the potential role that sign language proficiency may play on the capacity of the AC of the congenitally deaf to represent visual content. Our two groups of participants differed not only on their hearing capacity, but also in their proficiency in using sign language – deaf individuals were proficient in using sign language, whereas hearing participants here not. Extant data on visual processing under deafness strongly suggests, however, that the majority of effects indicating visual processing in the AC of congenitally deaf individuals are due to auditory deprivation rather than to the use of sign language (e.g., Fine, Finney, Boynton & Dobkins, 2005; for similar results see also Bavelier et al., 2000; Neville & Lawson, 1987b).

Another outstanding issue concerns how visual information reaches the AC of congenitally deaf individuals. One possible pathway involves (visual and auditory) subcortical nuclei. Roe *et al*. (1990) suggested that auditory thalamic nuclei may be involved in delivering visual information to deafferented A1. Work in the barn owl may also suggest that mixing of auditory and visual information at the level of the colliculus could provide a means for how AC could come to represent crude organizational principles for visual information in the congenitally deaf (e.g., Brainard & Knudsen, 1993). Moreover, Barone, Lacassagne & Kral (2013) showed that A1 of deaf cats receives a (weak) projection from visual thalamus. Thus, it could be that there is an 'unmasking' effect of congenital deafferentation in AC, such that the integration of auditory and visual information occurring in the midbrain is projected into the auditory cortex. Interestingly, it has been shown that the lateral geniculate nucleus (a thalamic relay of visual information to and from the cortex; LGN) over-represents the horizontal plane when compared to the vertical one (e.g., Schneider, Richter, & Kastner, 2004) - and this could be the basis for our differential decoding results for vertical and horizontal planes. Another possibility may relate to existing cortico-cortical connections between primary auditory and visual cortices. Bavelier & Neville (2002) suggested that the degeneration of these connections due to deafness could be responsible for a special involvement of AC in compensatory plasticity and for the observed advantage for processing peripheral stimuli in the congenitally deaf.

Finally, our data may have important implications for neuroprosthetics (e.g., cochlear implants). The implementation of those devices depends on exploiting the content of the representations within the deprived sensory system. The neuroplastic reorganization demonstrated here – and in particular the neuroplastically induced representation of visual content – may be ineffective in processing auditory input arriving from newly implanted devices, leading to complications in the implementation of those devices (e.g., Sandmann *et al*., 2012).

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SUPPLEMENTARY ONLINE MATERIAL

S1 – Univariate analysis.

S2 – Example of between-subject MVPA.

S3 – What is the locus of neuroplastic changes happening within the AC of congenitally deaf individuals?

Fig. S1 – Univariate whole-brain analysis of the representation of the azimuth and medial planes

S1. Univariate analysis.

We performed univariate analysis on our visual data within the deaf and hearing groups. We first did a region-of-interest univariate analysis over the data from our experiment, and showed that for deaf but not hearing participants, the contrast between the inner-most and the outer-most annuli yielded activation in AC (bilateral, t (3080) = 1.85, p = 0.064; right hemisphere AC, t (3080) = 1.97, p = 0.048). Moreover, the contrast between locations within the azimuth plane (i.e., left vs right) yielded marginally significant activations in right AC (t (3080) = 1.90, p = 0.058), whereas the contrast between positions within the medial plane (i.e., up vs. down) did not (t (3080) = 0.66, p = 0.511).

We then performed whole-brain analyses. For the deaf, but not for the hearing, contrasting left *versus* right presentations (i.e., the azimuth plane condition) led to activation within superior temporal and parietal regions. Contrasting superior *versus* inferior visual presentations (i.e., the medial plane) led to a much less widespread pattern of activation throughout temporal and parietal cortices, within both deaf and hearing participants. Finally, contrasting central to peripheral locations showed a widespread activation in superior parietal regions for both groups, and some temporal and temporo-parietal activation (more in the right hemisphere) for the deaf.

These data show, as demonstrated before (e.g., Finney et al., 2001), that there is a neural processing advantage for items presented in the periphery within the auditory cortex of deaf individuals, and that this is especially prevalent within the right auditory cortex. These data also hint at the fact that this advantage may be restricted to items presented within the azimuth plane.

S2. Example of between-subject MVPA.

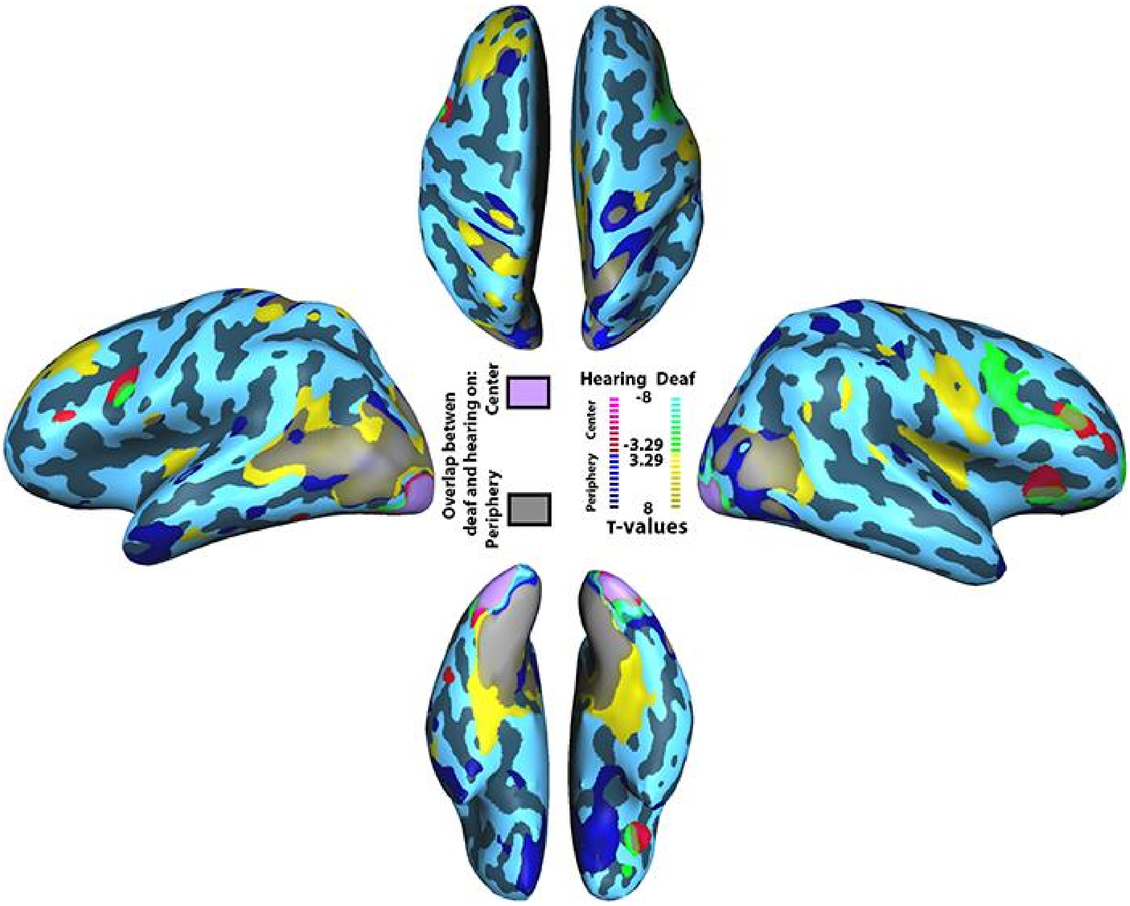
To better explain the way in which we analyzed our between-subject MVPA data, we will present an example for within-group classification performed over data from the AC of congenitally deaf individuals regarding the classification “center versus periphery”. We conducted MVPA to investigate the possibility of dissociating activation patterns arising as a response to centrally presented visual stimuli (i.e., the 2 most central rings) from those arising as a response to peripherally presented visual stimuli (i.e., the two most peripheral rings). We trained the classifier to predict whether the activation patterns were related with “central” or “peripheral” visual stimuli on beta values from 8 deaf participants (10 beta values times 2 categories times 8 subjects for a total of 160 pattern vectors), and tested the model over beta values from the remaining 2 deaf participants (10 beta values times 2 categories times 2 subject for a total of 40 pattern vectors; Haxby *et al.*, 2001, 2011).

S3. What is the locus of neuroplastic changes happening within the AC of congenitally deaf individuals?

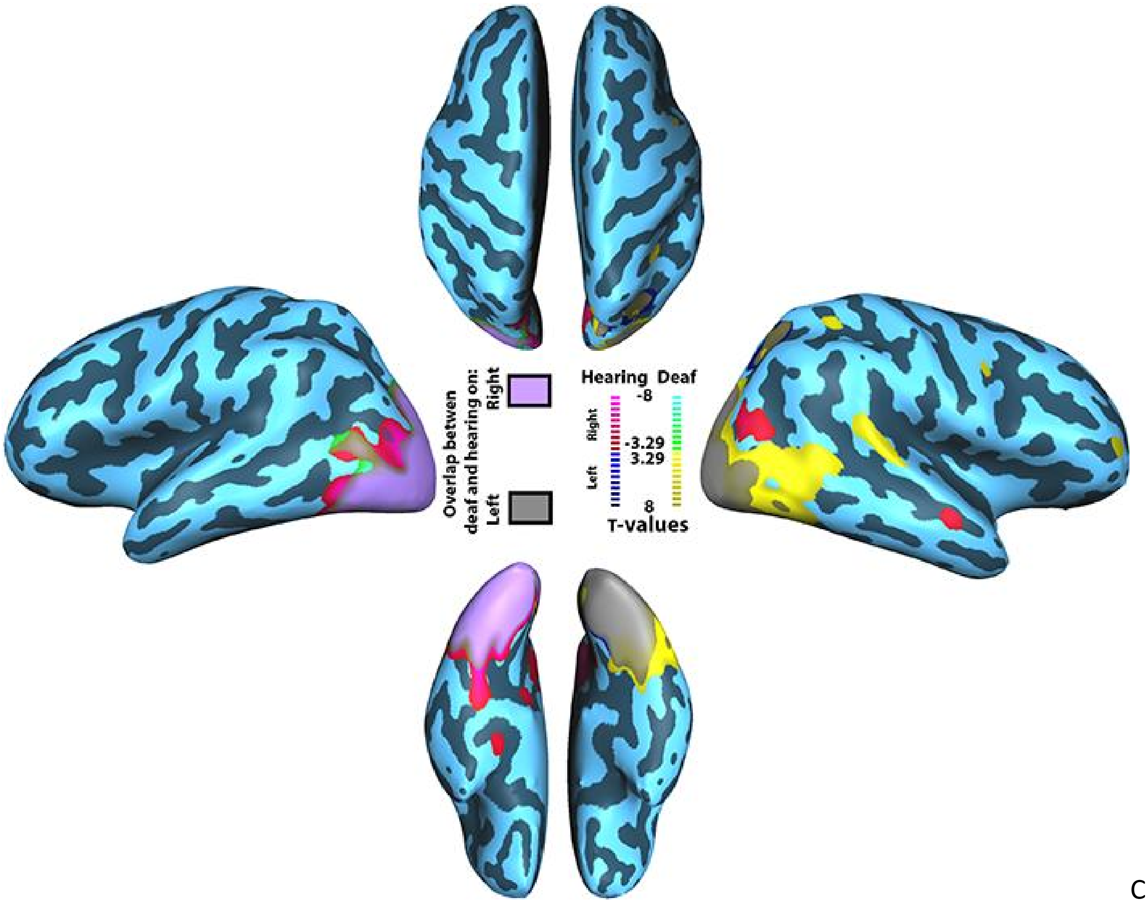
Prior findings implicate several auditory areas, but leave the role of PAC, and in particular A1, underdetermined in congenitally deaf humans. Some reports showed that A1 responds to visual stimulation both in human and non-human subjects (e.g., Finney et al., 2001; Hunt et al., 2006; Roe et al., 1990). Many others, however, have failed to show any visual responses in A1 (e.g., Hickok et al., 1997; Kral et al., 2003; Nishimura et al., 1999; Stewart and Starr, 1970). Moreover, it seems that A1 in deaf animals still responds to electric stimulation of the auditory nerve (e.g., Hartmann et al., 1997), suggesting that A1 may not go through massive reorganization under deafness. Nevertheless, given the coordinates of our auditory region, it seems that our activation is within PAC, alongside activation in non-core auditory regions.

Fig. S1 – Univariate whole-brain analysis of the representation of center and periphery, as well as the azimuth and medial planes. Contrast (t-values) maps for the contrasts of interest. (A) Contrast maps for center versus periphery locations across the whole-brain for deaf and hearing participants; (B) Contrast maps for left versus right locations across the whole-brain for deaf and hearing participants; and (C) Contrast maps for up versus down locations across the whole-brain for deaf and hearing participants. Contrast maps are cluster corrected 0.001.

A.



B.


Overlap betwen deaf and hearing on:
Right
Left
Hearing
Deaf
Right
Left
-8
-3.29
3.29
8
T-values

C.

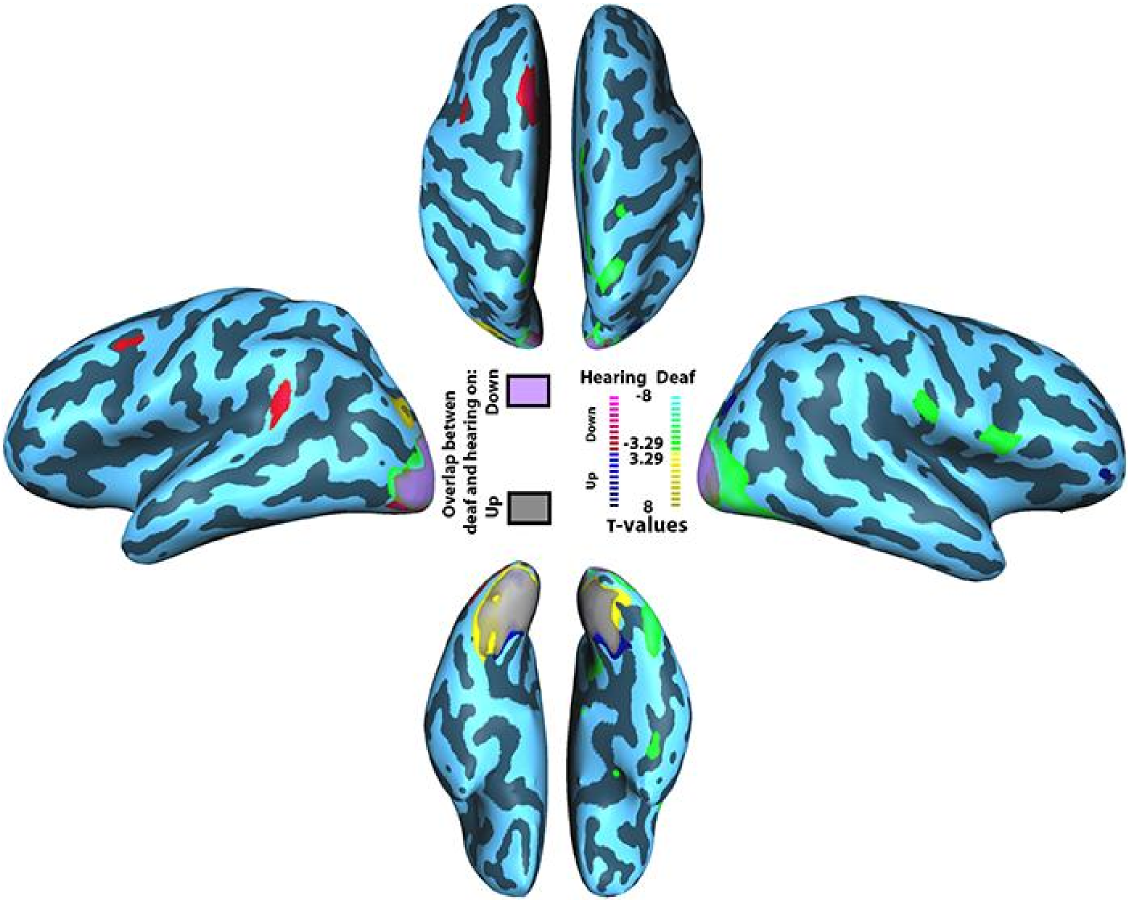

Overlap betwen deaf and hearing on:
Down
Up
Hearing
Deaf
Down
Up
-8
-3.29
3.29
8
T-values

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FIGURE LEGENDS

Figure 1. Stimuli used in the experiments. (**A**) stimuli used for visual field location classification; and (**B**) stimuli used for eccentricity classification.

Figure 2. Auditory and visual cortex. (**A**) Regions within auditory cortex (AC), defined in hearing participants, and primary visual cortex used for the classification. (**B**) The auditory cortex ROI includes de Heschl's Gyrus (Brodmann Area 41), but does not include other auditory regions of interest such as Brodmann Areas 42 and 22. *t* map corresponds to the AC ROI contrast of white noise vs. silence . HG – Heschl's Gyrus; SF – Sylvian Fissure; STG – Superior Temporal Gyrus; STS – Superior Temporal Sulcus.

Figure 3. Percent correct performance for real and surrogate data in auditory cortex (bilaterally) and visual cortex. (**A**) Percent correct performance for quadrant classification in AC; and (**B**) Percent correct performance for the classification of the contrasts left vs. right and up vs. down in AC; (**C**) Percent correct performance for quadrant classification in V1; and (**D**) Percent correct performance for the classification of the contrasts left vs. right and up vs. down in V1. Bars correspond to performance with real data, and black dashes (**-**) correspond to performance with the surrogate data. Dashed lines correspond to different confidence intervals for the estimate of the mean of the surrogate data. Red error bars correspond to the SEM of the classification data, whereas black error bars correspond to the SEM of the surrogate data. Within-group classification performance for deaf individuals is above chance for quadrant classification, demonstrating that visual location is represented in the AC of congenitally deaf individuals. Stimuli within the azimuth, when compared to stimuli within the meridian plane, seem to drive responses in AC of congenitally deaf individuals. Results in V1 show highly significant classification performance across classifiers.

Figure 4. Whole-brain searchlight classification accuracy for center/periphery locations, and locations within the azimuth and meridian planes. (A) Decoding performance effect maps (z-values) for decoding center versus periphery locations across the whole-brain for deaf and hearing participants; **(B)** Decoding performance effect maps (z-values) for decoding left versus right locations across the whole-brain for deaf and hearing participants; and **(C)** Decoding performance effect maps

(z-values) for decoding up versus down across the whole-brain for deaf and hearing participants. z-values (calculated against surrogate data) above 3.9 correspond to p-values equal to or less than 0.0001; Decoding performance for the deaf group is represented in yellow, whereas for the hearing group it is represented in blue. Overlap in decoding ability for both groups in represented in silver gray.

Figure 1. Stimuli used in the experiments.

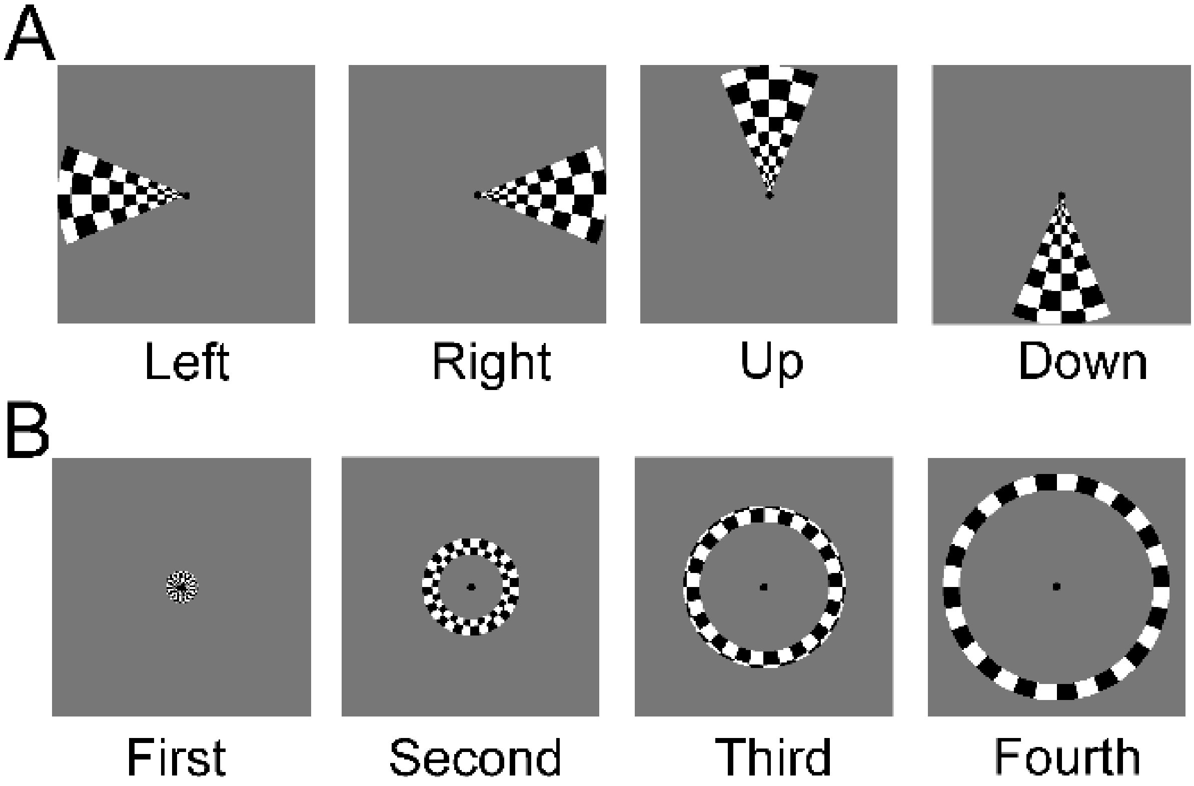
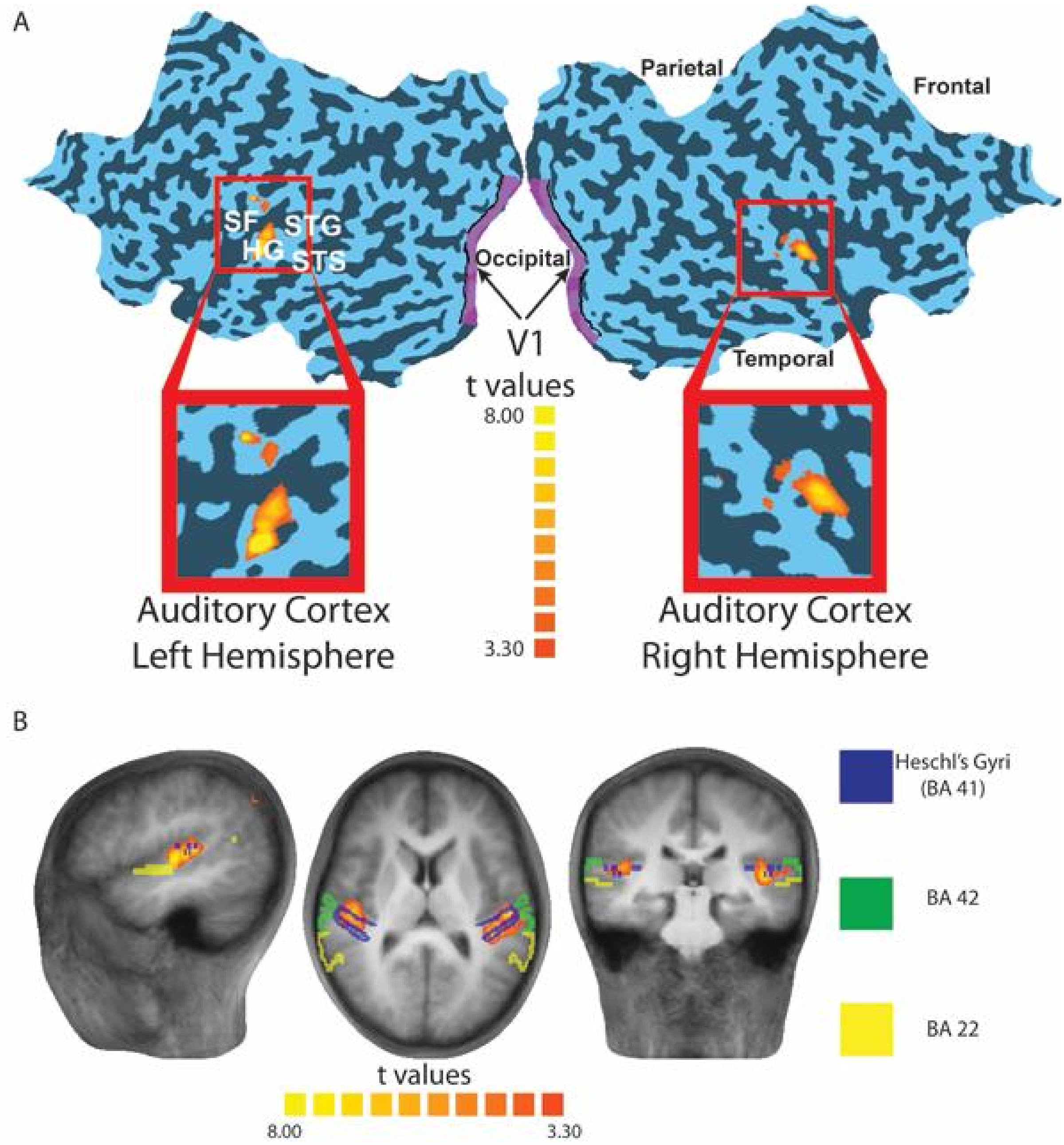


Figure 2. Auditory and visual cortex.



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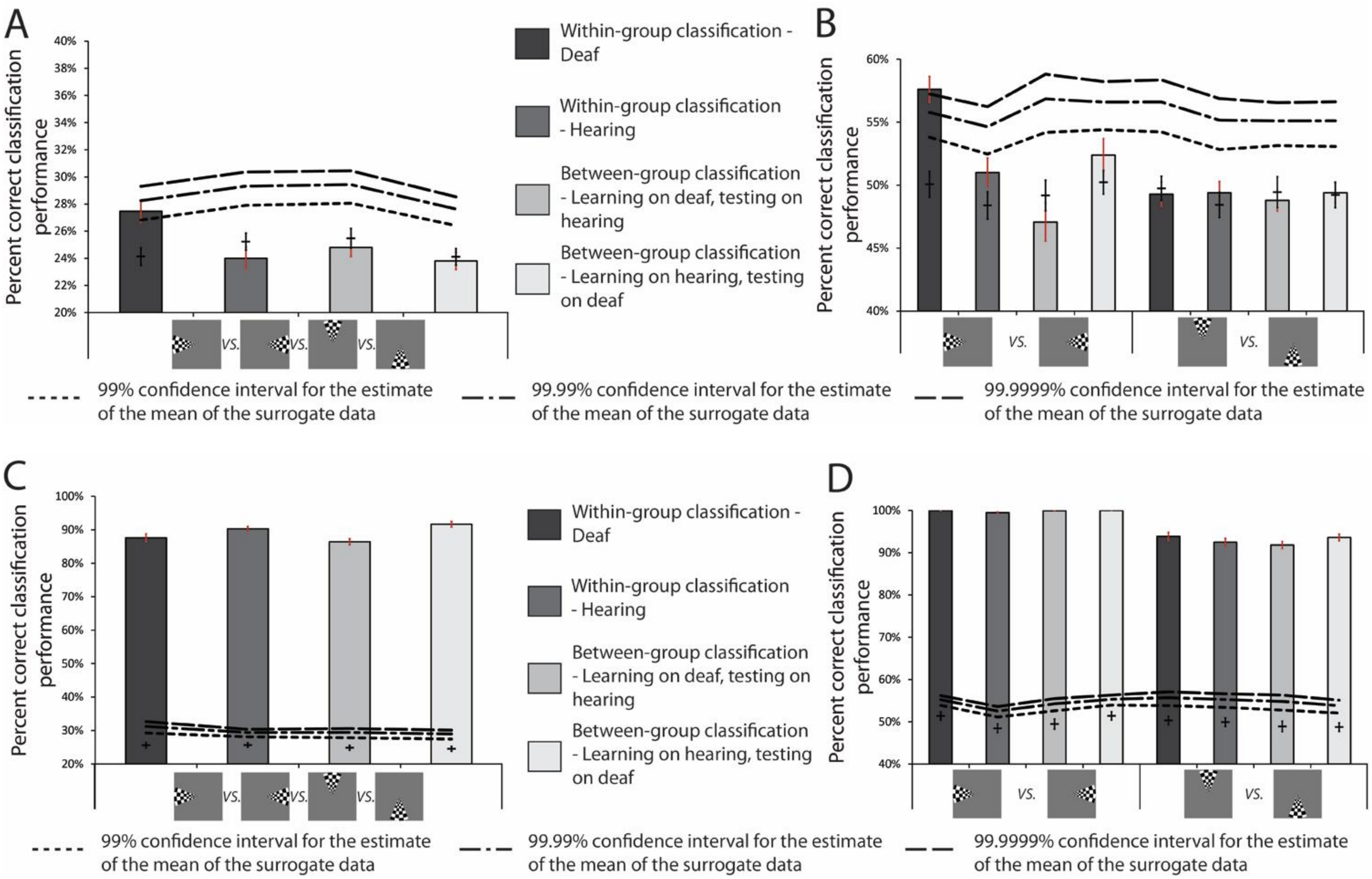
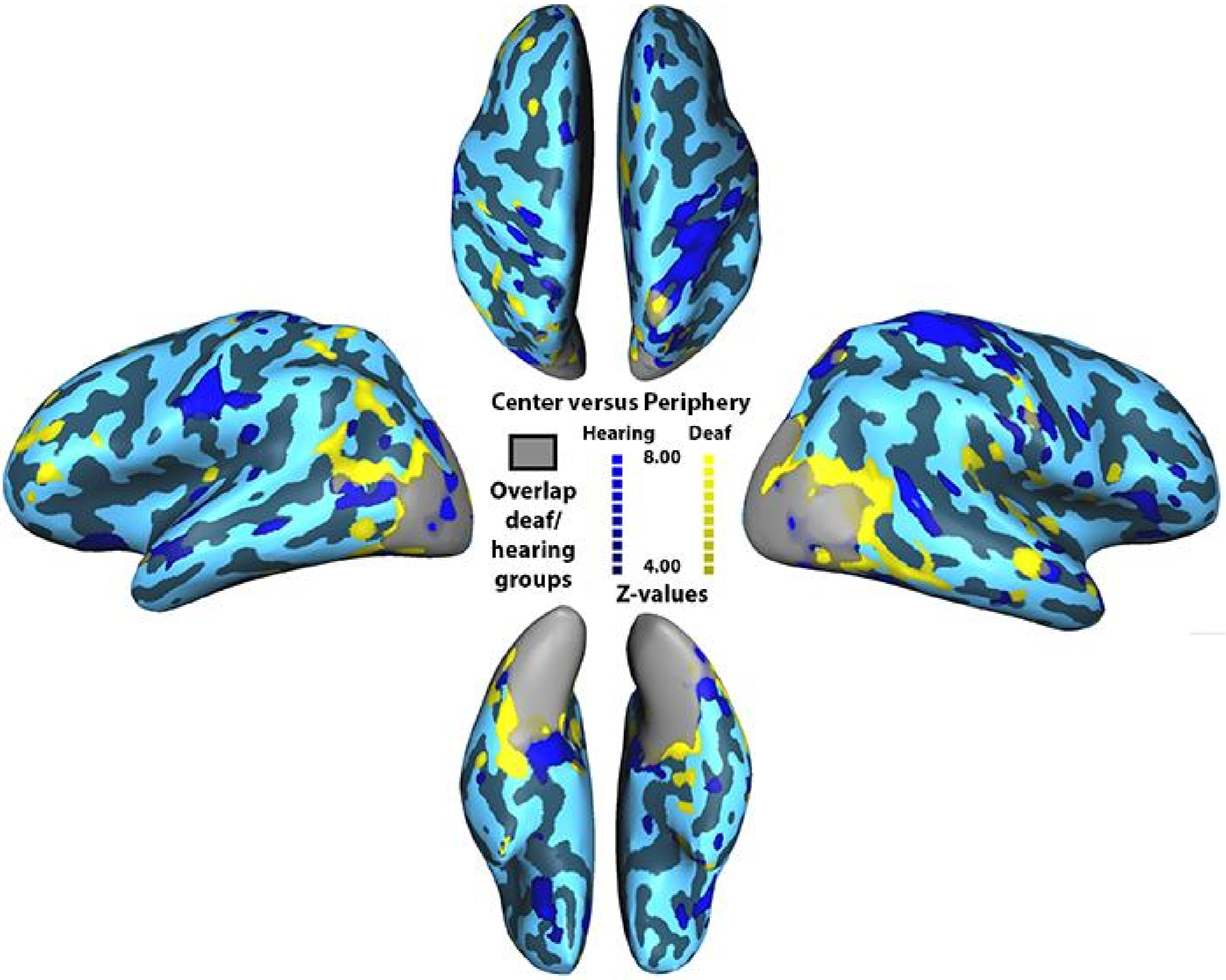


Figure 4. Whole-brain searchlight classification accuracy for center/periphery locations, and locations within the azimuth and meridian planes.

A.



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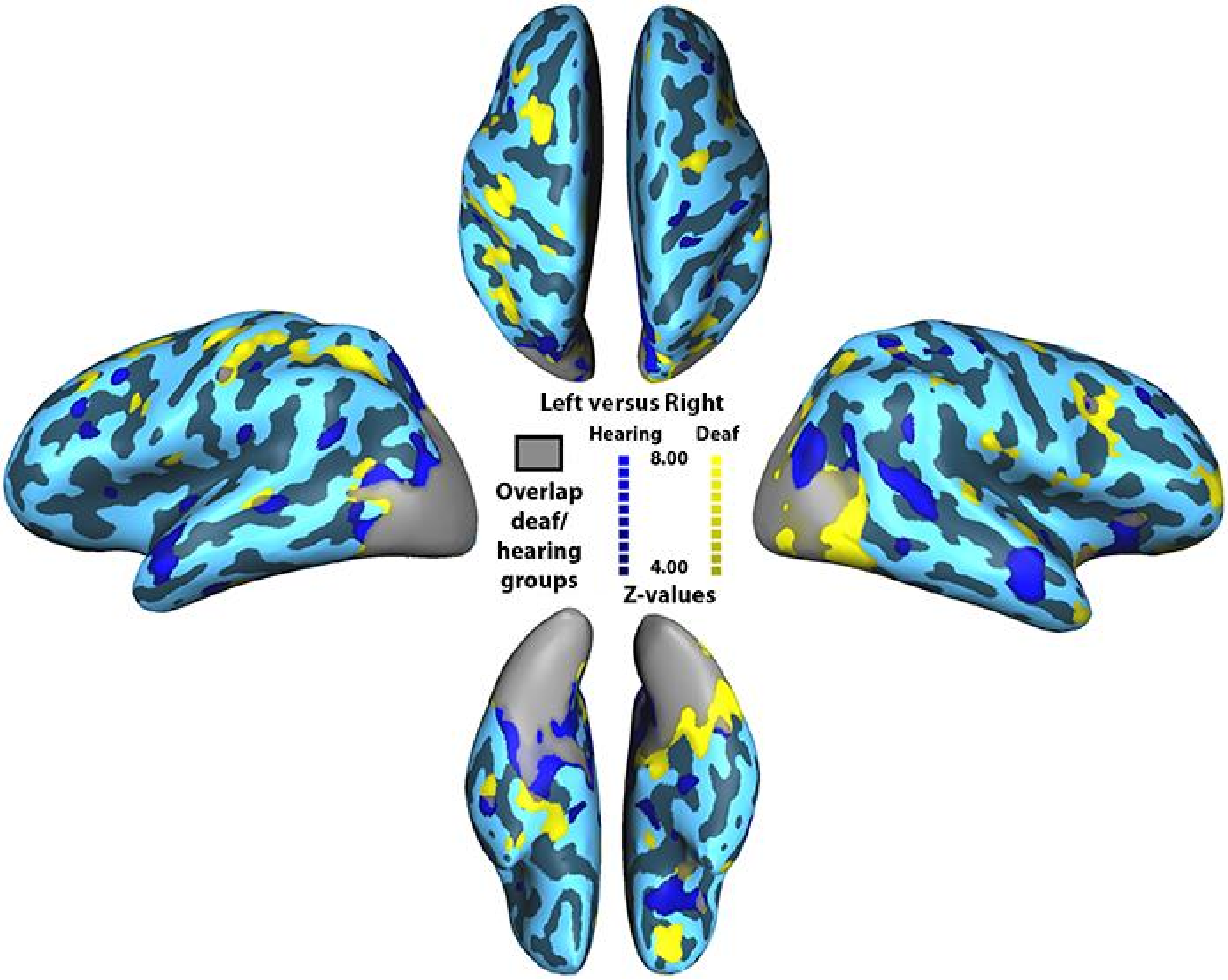
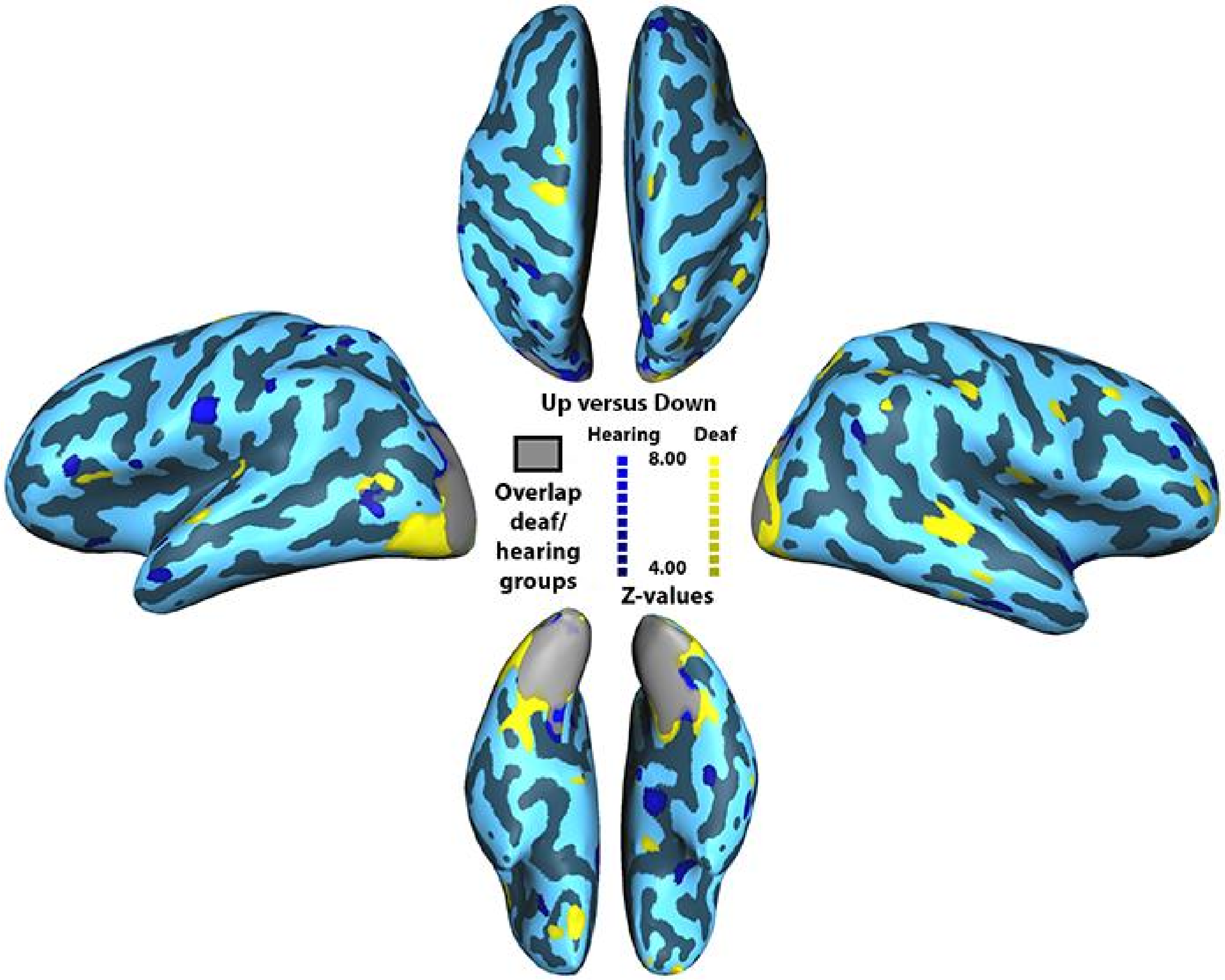

Left versus Right
Hearing
Deaf
8.00
4.00
Z-values
Overlap deaf/ hearing groups

C.


Up versus Down
Hearing
Deaf
8.00
4.00
Z-values
Overlap deaf/ hearing groups