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Reorganization of neural systems mediating peripheral visual selective attention in the deaf: An optical imaging study

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Abstract

Theories of brain plasticity propose that, in the absence of input from the preferred sensory modality, some specialized brain areas may be recruited when processing information from other modalities, which may result in improved performance. The Useful Field of View task has previously been used to demonstrate that early deafness positively impacts peripheral visual attention. The current study sought to determine the neural changes associated with those deafness-related enhancements in visual performance. Based on previous findings, we hypothesized that recruitment of posterior portions of Brodmann area 22, a brain region most commonly associated with auditory processing, would be correlated with peripheral selective attention as measured using the Useful Field of View task. We report data from severe to profoundly deaf adults and normal-hearing controls who performed the Useful Field of View task while cortical activity was recorded using the event-related optical signal. Behavioral performance, obtained in a separate session, showed that deaf subjects had lower thresholds (i.e., better performance) on the Useful Field of View task. The event-related optical data indicated greater activity for the deaf adults than for the normal-hearing controls during the task in the posterior portion of Brodmann area 22 in the right hemisphere. Furthermore, the behavioral thresholds correlated significantly with this neural activity. This work provides further support for the hypothesis that cross-modal plasticity in deaf individuals appears in higher-order auditory cortices, whereas no similar evidence was obtained for primary auditory areas. It is also the only neuroimaging study to date that has linked deaf-related changes in the right temporal lobe to visual task performance outside of the imaging environment. The event-related optical signal is a valuable technique for studying cross-modal plasticity in deaf humans. The non-invasive and relatively quiet characteristics of this technique have great potential utility in research with clinical populations such as deaf children and adults who have received cochlear or auditory brainstem implants.

Keywords: deafness, event-related optical signal, optical imaging, Useful Field of View, visual attention, Brodmann area 22

Abbreviations

ASL, American Sign Language; BA, Brodmann area; CI, cochlear implant; EROS, event-related optical signal; fMRI, functional magnetic resonance imaging; fNIRS, functional near infrared spectroscopy; HG, Heschl's gyrus; HL, hearing loss; IOI, interval-of-interest; KBIT-2; Kaufmann Brief Intelligence Test 2; LH, left hemisphere; MEG, magnetoencephalography; NH, normal-hearing; NIR, near infrared; NVIQ, non-verbal intelligence quotient; PPC, posterior parietal cortex; pSTS, posterior superior temporal sulcus; PT, planum temporale; PTA, pure tone average; RH, right hemisphere; ROI, region-of-interest; STG, superior temporal gyrus; TMS, transcranial magnetic stimulation; UFOV, Useful Field of View

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1. Introduction

Neuroplasticity is the brain's ability to adapt, both structurally and functionally, to unique environmental situations. This is a defining characteristic of neural systems, but one that is also poorly understood at the systems level. One approach to characterizing experience-dependent neuroplasticity is to consider differences between individuals with typical sensory experience and those who are missing certain sensory inputs, such as deaf or blind individuals. Specifically, it is possible that different input modalities (such as sight and hearing) might compete for the recruitment of some brain regions that are not exceedingly specialized, such as secondary sensory areas. In this case, the chronic absence of input from one of these modalities might modify the most commonly observed balance between the competing modalities. For instance, in the absence of hearing, an area that is commonly recruited during auditory processing may instead be recruited during visual processing. This might provide a processing advantage in the spared modality for people in whom input from another modality is lost (e.g., an advantage in auditory processing for blind individuals, or in visual processing for deaf individuals; see Frasnelli et al., 2011 for a review of behavioral changes associated with sensory loss). Thus, by determining how neural systems reorganize in the face of sensory deprivation, researchers can explore the structural, functional, and temporal limits of experience-dependent plasticity. In the current study we focus on the possibility that recruitment of brain areas, typically used by hearing individuals to process auditory information, might be correlated in deaf individuals with an advantage during the performance of a visual task.

Many studies have reported enhanced visual task performance in deaf individuals, with the majority of these studies employing either attention-demanding tasks in which stimuli are presented in the visual periphery (Buckley et al., 2010; Codina et al., 2011; Dye, et al., 2009; Proksch & Bavelier, 2002; Stevens & Neville, 2006) or tasks that involve processing of visual motion in the periphery (Armstrong et al., 2002; Bosworth & Dobkins, 2002ab; Bosworth et al., 2013; Hauthal et al., 2013). This suggests that this experience-dependent processing advantage only occurs for certain specialized tasks. Deaf individuals are also more distracted by peripheral distractors when attending to the central visual field than by central distractors when attending to the peripheral visual field, while the opposite pattern is observed in hearing individuals (Dye et al., 2007; Proksch & Bavelier, 2002; Rothpletz et al., 2003; Sladen et al., 2005; for recent reviews of changes in visual functions in deaf individuals see Dye & Bavelier, 2013, and Pavani & Bottari, 2011). In contrast to these changes for attention-demanding tasks with peripheral stimuli, deaf and hearing individuals do not appear to differ in their basic visual sensory thresholds on tasks such as motion detection and contrast

sensitivity (Bosworth & Dobkins, 1999; Bosworth & Dobkins, 2002a; Brozinsky, & Bavelier, 2004; Finney & Dobkins, 2000). Finally, by comparing deaf signers and non-signers to hearing signers and non-signers, several studies have shown that these specific enhancements in visual function are likely due to deafness and not the use of visual-gestural languages such as ASL (Bavelier et al., 2001; Bosworth & Dobkins, 2002ab; Dye et al., 2009; Neville & Lawson, 1987), which might have been hypothesized to engage and sensitize peripheral visual attention.

In parallel to this behavioral work, several neuroimaging studies have compared cortical recruitment in deaf and hearing adults during tasks that require processing of non-linguistic visual stimuli. Many of these studies have reported differential activation of cortical areas normally considered to be auditory or auditory association areas. In one of the earliest such studies, Bavelier et al. (2001) examined visual motion processing in deaf signers of ASL, hearing non-signers, and hearing signers of ASL. In addition to several changes in motion processing pathways, Bavelier and colleagues reported that deafness resulted in enhanced recruitment of pSTS during a motion discrimination task performed while observing moving dot displays. This effect was not observed in hearing signers, suggesting that it was driven by deafness, and might have been the result of increased innervation of multisensory association areas in the absence of competing auditory inputs. Finney et al. (2001) also presented deaf and hearing adults with moving dot stimuli, asking them to attend to the displays in order to detect brief changes in luminance. They defined auditory ROIs by presenting the hearing adults with musical stimuli. The resulting ROIs were located in Brodmann areas 22, 41, and 42 bilaterally, representing primary auditory and auditory association cortices. They restricted their analysis of subsequent visually-evoked cortical responses to these auditory ROIs, reporting that visual motion stimuli activated all these areas more in deaf than in hearing adults, with the effect observed only in the RH. A subsequent study from the same group used MEG to ask, with increased temporal resolution, whether this cross-modal recruitment of auditory areas by visual inputs reflected early sensory processing or later attentional (top-down) effects (Finney et al., 2003). They reported recruitment of core auditory areas (BA 41/42) in the RH within 100 to 400ms of stimulus presentation, leading them to suggest that the cross-modal activation reflected early sensory processing, possibly via direct connections from the visual thalamus to auditory cortex.

A study by Sadato et al. (2005) compared the cortical responses of deaf and hearing adults to various types of linguistic and non-linguistic visual stimuli. Whereas sign language stimuli resulted in enhanced recruitment of the left PT in deaf signers, moving dot stimuli led to enhanced recruitment of the PT in the superior temporal gyrus of the RH. Fine et al. (2005) employed a luminance change

detection task while deaf and hearing participants observed moving dot stimuli during fMRI. They reported enhanced recruitment of core auditory and neighboring auditory association cortex (BA22, and BA41/42) in the deaf, with the effect larger during attend-motion than during ignore-motion conditions. Vachon et al. (2013) asked deaf and hearing adults to attend to moving dots and perform either a form-from-motion task (designed to recruit the ventral “what” processing stream) or a motion direction discrimination task (designed to recruit the dorsal “where” stream). For both tasks, deaf adults recruited auditory association areas (BA21/22) more than did the hearing controls. They concluded that cross-modal recruitment of core auditory or auditory association areas by visual inputs was not restricted to the dorsal visual pathway, but that it could also be observed in tasks based upon visual form. Scott et al. (2014) presented subjects with flickering visual stimuli in the perifovea and periphery, and found that deaf participants recruited HG, superior temporal areas, and the PPC, with greater recruitment for peripheral than for perifoveal stimulation. This trend was not observed in the hearing participants. More recently, Dewey and Hartley (2015) reported an fNIRS study where deaf and hearing adults were presented with coherent motion in the periphery. Only deaf subjects showed significant increases in hemodynamic recruitment in a RH auditory ROI consisting of HG and the STG. Finally, a recent study by Almeida et al. (2015) used voxel-pattern analysis of fMRI data to show that activity in a bilateral auditory ROI (encompassing BA41 as well as some parts of BA42 and BA22) could be used for above-chance prediction of the left-right location of a visual checkerboard pattern in deaf, but not in hearing, participants. In addition, the pattern of activation within the RH could be used to decode whether the stimulus was presented in central or in peripheral vision. For a review of the neural changes seen in the deaf, see Bavelier, Dye, & Hauser, (2006). For a more general review of cross-modal plasticity, see Merabet & Pascual-Leone (2010) and Pascual-Leone, et al. (2005).

From these studies it seems clear that early profound deafness results in a cross-modal reorganization of brain function. The RH of deaf adults, and in particular areas in the temporal cortices assumed to be unimodal auditory or auditory association areas in normally-hearing individuals, gain access to information from the visual modality and participate in the processing of visual stimuli. However, it remains unclear what the functions of these cortical areas are in visual processing. Auditory association areas such as the PT in the RH have been reported to perform the computations required for auditory object selection and/or localization (Ahveninen et al., 2013; Hirnstein et al., 2013; Rauschecker & Tian, 2000). Perhaps, in the absence of auditory inputs, these areas may perform the same computational function using only visual afferents (Kok et al. 2014; Lomber et al., 2010;

Meredith et al., 2012). Whatever their exact function, however, the recruitment of auditory areas during visual processing might be expected to be associated with a visual performance improvement. A question that could be raised is whether the difference in the recruitment of auditory cortical areas in visual processing in deaf vs. hearing people is best described as quantitative (i.e., activity in these areas occurs more in deaf than hearing people) or qualitative (i.e., activity in these areas only occurs in deaf but not in hearing people). This question is difficult to address (it may involve a test of the null hypothesis), but the most reasonable approach is to determine whether activity in these regions in normal people is above a baseline level or not. Unfortunately, only a portion of studies presented reported such a test. Of those that did (e.g., Finney et al., 2001, 2003; Scott et al., 2014; Dewey & Hartley, 2015; Almeida et al., 2015) the general consensus is that activity in normal hearing people in the relevant region is not above baseline. Thus the results suggest that the phenomenon is a qualitative one. However, in the current study we will investigate both regions that are not expected to be activated by visual stimuli in hearing people (such as primary and associative auditory cortex), and area that may be active in all participants (such as V1/V2).

The purpose of the current study was to use EROS to study differences in cortical function between deaf adults and NH controls, and to examine the relationship between deaf-hearing differences in neural recruitment and their performance on a peripheral visual attention task. EROS is a non-invasive functional imaging method based on NIR light, and it possesses a ms level temporal resolution and cm level spatial resolution (Gratton & Fabiani, 2010). Non-invasive optical imaging measures changes in the absorption and scattering of NIR light travelling through cortical tissue from a light source to a nearby detector. Swelling and shrinking of neurons is associated with neuronal depolarization and hyperpolarization, giving rise to variations in tissue scattering (Foust & Rector, 2007). Time-of-flight changes for the photons are therefore measured as phase-delays (Gratton & Fabiani, 2012). Using frequency domain oximeters, pulsating NIR light is projected through the scalp and into the cortex via fiber optic cables, to detectors also positioned on the scalp, at a range of distances away from the source. Each detector may receive light from multiple sources, resulting in many source-detector pairings, or channels, of light paths through the brain. Channels are therefore time-multiplexed to distinguish them from one another. The path of light through the tissue can be mathematically modeled on an individual basis using information about the arrangement of light sources and detectors on each individual participant's scalp coupled with known estimates of baseline absorption and scattering of head tissues (Gratton, et al., 1994; Gratton & Fabiani, 2010).

We collected EROS data using a high-density optical montage, covering most of the scalp, from deaf adults and NH controls while they performed a complex visual attention task based upon the UFOV task reported by Dye et al. (2009). We predicted that cross-modal plasticity resulting from congenital, profound deafness would result in the recruitment of core auditory areas in the RH temporal lobe during performance of this task – the classic hallmark of ‘strong’ cross-modal plasticity: activation of a unimodal auditory area by visual inputs. We also predicted increased activation of multimodal association areas in the right hemisphere in deaf individuals, reflective of inter-sensory competition for processing resources being dominated by visual inputs in individuals with auditory deprivation (‘weak’ cross-modal plasticity). In addition, using the temporal resolution provided by EROS data, we conducted exploratory analyses to determine the temporal latency of cross-modal recruitment of RH temporal regions. Finally, we examined the relationship between recruitment of auditory regions for visual processing in deaf individuals and their accuracy thresholds on the UFOV task using behavioral data collected on a separate occasion.

2. Materials and methods

2.1 Participants

This study was approved by the Institutional Review Board at the University of Illinois at Urbana-Champaign and informed consent was obtained from all participants, who were compensated for their participation. To be included in this study, participants were required to either have a PTA HL in their better ear greater than 80dB (deaf adults) or normal-hearing without correction (NH controls), and to be aged between 18 and 50 years. Participants were excluded from participation if they had impaired vision that couldn’t be corrected using corrective lenses; a standardized NVIQ score less than 80; a history of major neurological disorder; played action video games more than 5 hours per week; or wore a cochlear implant or other kind of implantable device that precluded a magnetic resonance imaging scan.

2.1.1 Deaf adults

Thirteen deaf individuals participated in the study (recruited from communities in Illinois and Indiana). Three individuals were excluded from all reported analyses. One was lost due to technical issues during the behavioral testing session and two were excluded because their behavioral threshold scores were greater than three standard deviations from the grand mean across subjects.

The remaining 10 deaf participants, seven males and three females, had a mean age of 34.7 years (SD = 11.0) and a mean NVIQ of 108.2 (SD = 14.2) as determined by the K-BIT2 (Kaufman & Kaufman,

2004). Based upon audiological examination, all deaf participants were severe-to-profoundly deaf in both ears. The mean pure tone average hearing loss (PTA HL) in the most sensitive ear for nine deaf participants was 101.5 dB (SD = 7.9) with audiological data missing from one deaf participant, who self-reported profound deafness (participant D4 in Tables 1&2). Further information about deaf participants is provided in Table 1, and a group audiological profile is provided in Figure 1.

One additional deaf participant was excluded from the EROS session analyses (behavioral and optical) due to data loss from equipment malfunction.

2.1.2 NH controls

Eleven hearing individuals participated in the study (recruited through e-mails to the faculty and staff of the University of Illinois at Urbana-Champaign) to serve as a NH control group. This group consisted of four males and seven females, with a mean age of 30.8 years (SD = 8.1) and a mean NVIQ of 113.1 (SD = 13.5) as determined by the K-BIT2. For these eleven participants, the mean PTA HL in the most sensitive ear was 3.5 dB (SD = 5.1).

There were no statistically significant differences between the deaf participants and NH controls on age ($t(19) = 0.93$, $p = .365$), IQ ($t(19) = -1.08$, $p = .296$), or gender distribution ($\chi^2(1) = 2.38$, $p = .123$). As expected, the NH controls did have significantly lower PTA HL than the deaf participants ($t(13) = 32.22$, $p < 0.001$).

Two NH participants were excluded from the EROS session analyses (behavioral and optical) due to data loss from equipment malfunction. Thus, for the brain imaging portion of the study, there were 9 deaf and 9 NH participants.

For a full breakdown of which participants were included in which portions of the study, please see Table 2.

2.3 Design

Participants completed one behavioral testing session, two EROS sessions on separate days, a structural MR scan, and audiological testing. All sessions were completed within a one-month period. These protocols occurred in a variable order, according to participants' schedules.

2.4 Procedure

2.4.1 Behavioral testing

The following behavioral sub-tasks were conducted in a separate session from the EROS imaging sessions. Each task represents one component of the UFOV, and these sub-tasks were administered in the order they appear here.

2.4.1.1 Central discrimination

The central discrimination task measures a participant's ability to discriminate between one of two visual images presented rapidly at the center of the screen. Our previous work has shown that while performance on this task does not vary as a function of deafness (Dye et al., 2009), poor performance may be indicative of a poor attention at fixation which is required by subsequent sub-tasks (Dye, 2016). Therefore, this task was used as exclusion criteria to avoid confounds of participants performing poorly on the experimental task due to more general attention difficulties.

Stimuli were presented on a touch screen connected to a MacBook Pro laptop running Matlab and the Psychophysics Toolbox (PT-3) under Mac OS X. The stimulus was a cartoon face subtending 2.0 degrees of visual angle with either long (0.27 degrees of visual angle) or short (0.16 degrees of visual angle) hair presented at fixation in the center of the screen (Figure 2A). The task required participants to respond to each stimulus by saying "short" or "long" (NH controls) or fingerspelling S or L (deaf adults).

The stimulus duration was varied trial-to-trial according to a three-down one-up staircase procedure with adjustments of +/- one monitor refresh frame (at 60 Hz), with no maximum duration. A brief, white visual noise mask followed all stimuli. Stimulus presentation continued until one of the following stopping conditions was satisfied: (i) twelve reversals (changes from ascending to descending the staircase) occurred, (ii) the participant gave 10 correct responses in a row at a presentation duration of one frame, or (iii) 72 trials were completed. Thresholds were computed as the average stimulus duration for the final eight reversals, or, if the participant had 10 correct responses at one frame, their threshold was set to one frame.

2.4.1.2 Central discrimination plus peripheral localization

This second sub-task served the purpose of screening out participants with problems meeting dual task requirements of the main UFOV subtask. Since it does not include distractors, we did not expect differences between deaf adults and NH controls. Similar to the central-only task, this task was used as exclusion criteria to avoid confounds of participants performing poorly on the experimental task due to more general attention difficulties. The task requires participants to perform the central discrimination task (described above) concurrently with a peripheral localization task (Figure 2B).

The peripheral target was a line drawing of a diamond (subtending 2 degrees of visual angle) presented along one of the four inter-cardinal axes at 20 degrees of visual angle from fixation. Following the simultaneous presentation of the central and peripheral stimuli, a white noise mask covered the screen, followed by a response screen. After making a response to the central target, participants were instructed to indicate the peripheral target location by touching the corresponding location on the touchscreen. The stimulus duration on each trial was the same for the central and peripheral targets, and again was varied trial-to-trial according to a three-down one-up staircase procedure with adjustments of +/- one monitor refresh frame (at 60 Hz). In order to be considered a correct response, participants had to respond correctly to both targets. The stopping procedure and threshold calculations were the same as in the first subtask.

2.4.1.3 Main UFOV task

The main UFOV task was the experimental behavioral task and is depicted in Figure 2C. It required participants to perform the central discrimination and peripheral localization tasks in the presence of distracting shapes presented along the four inter-cardinal axes at three different distances from fixation (6.67, 13.33 and 20 degrees of visual angle). The target was always presented at 20 degrees of visual angle, as in the previous task, and therefore in each display in addition to the central face there were four distractors at 6.67 degrees, four distractors at 13.33 degrees, 3 distractors at 20 degrees, and one target at 20 degrees.

While the stimulus duration was again varied trial-to-trial according to a three-down one-up staircase procedure with adjustments of +/- one monitor refresh frame (at 60 Hz), the procedure employed two such (interleaved) staircases. The central staircase determined stimulus duration on the basis of responses to the central stimulus, ignoring trials where the peripheral response was incorrect. The peripheral staircase varied as a function of accuracy on the peripheral task, ignoring trials where the central response was incorrect. Stimulus parameters for consecutive trials were selected from either the central or the peripheral staircases on a random basis. Trials from both staircases were presented until (i) eight reversals had occurred for both staircases, (ii) the participant gave 10 correct responses in a row at a presentation duration of one frame on both staircases, or (iii) 72 trials had occurred for both staircases. The stimulus durations at the eight reversals from each staircase were averaged to calculate central and peripheral thresholds unless, as in previous tasks, the participant had 10 correct trials in a row at one frame on either or both staircases, in which case the participant's threshold was set to one frame for that staircase.

The interleaved staircases were used to overcome a limitation of a similar procedure reported in Dye et al. (2009) whereby it was possible to generate a low peripheral localization threshold by ignoring the central target and then guessing its identity. Our focus here, however, is solely on the peripheral staircase threshold with the hypothesis that deaf individuals should perform better in this condition than NH controls. The central staircase threshold should not differ between the two groups, with abnormally high central staircase thresholds considered to be indicative of a lack of attention.

2.4.2 Structural MRI

Structural MRI data were collected from each participant on a Siemens 3T Trio scanner (T1-weighted image). A high resolution, 3D MPRAGE protocol was used, with a flip angle = 9° , TE = 2.32 ms, TR = 1900 ms, and inversion time = 900 ms. Slices were obtained in the sagittal plane (192 slices, .9 mm slice thickness, voxel size .9 x .9 x .9 mm) having matrix dimensions of 192 x 256 x 256 (in-plane interpolated at acquisition to 192 x 512 x 512) and field of view of 172.8 x 230 x 230 mm. The MR data were used to co-register the individual locations of the optical sources and detectors on the scalp with an individual's brain anatomy (Whalen et al., 2008; see also Chiarelli et al., 2015). Total scanning time was approximately 10-15 minutes, in which participants were instructed to lay as still as possible with their eyes closed for the duration of scanning.

2.4.3 Event-Related Optical Signal (EROS)

2.4.3.1 UFOV task

Participants performed a modified version of the main UFOV task while optical data were acquired. Rather than employing an adaptive staircase procedure, as in the behavioral testing, each stimulus had a fixed presentation duration of 68 ms¹. As presentation time was fixed, accuracy measures were used instead of perceptual thresholds. The presentation duration was chosen *a priori* based upon the thresholds reported in Dye et al. (2009). Specifically, this duration was selected with the aim of

¹ Our paradigm choices were dictated by having to compromise among different requirements. In the current case, previous behavioral experiments assessed performance on the UFOV task with thresholding measures. However, this varying presentation time would also result in different durations of stimulus presentation across groups – that, in the case of visual stimuli, translates into different intensities of the stimuli (because of the phenomenon of temporal integration due to retinal persistence) for the two groups. This creates a problem of interpretation of the difference in brain activity between the two groups. For this reason, we needed to fix stimulus duration for all subjects during the EROS recording. A second problem is that a large performance difference during the EROS session might lead to differences in movement-related activity. For instance, the type and/or latency of the response might be very different in the two groups. Again, this would complicate the interpretation of the EROS response: Would a difference in EROS activity between the two groups in a particular region be related to differential processing of the visual stimuli or to changes in the latency/amplitude of the motor responses? To avoid this potential confound, it is important to try and equate the motor part of the task. This led us to select a stimulus presentation time that generates relatively similar responses (in terms of time or accuracy) in the two groups.

obtaining similar task accuracy for deaf adult and NH control groups during measurement of optical signals.

The central discrimination task again had two possible hair lengths (short, long) while the peripheral localization used four possible target locations (NW, NE, SW, SE) and participants were asked to respond to both the central and the peripheral task. Each of these eight combinations was presented six times per block, resulting in blocks of 48 trials lasting approximately 4 minutes each. There were 15 such blocks per session, and two sessions, resulting in a total of 1440 trials. Stimuli were presented on a touchscreen connected to a PC running E-Prime. A Microsoft Sidewinder game controller was used to collect responses from participants. Participants used the A B X Y buttons to indicate target location, as these were approximately arranged in the same spatial fashion as the four possible target locations and therefore mapped well onto the response. Participants used the left and right trigger buttons on the back of the controller to indicate short or long hair on the central target. Assignment of short and long hair responses to these triggers was counterbalanced across participants.

2.4.3.2 EROS recording

EROS data was recorded using six synchronized frequency-domain Imagent oximeters (ISS, Inc., Champaign, IL). Sixty-four laser diodes shone 830-nm light modulated at 110 MHz into the brain through 400 micron silica optic fibers terminating on a custom-made, soft, foam helmet. This modulated light was picked up by 3-mm fiber-optic bundles also attached to the helmet, and transmitted to 24 photomultiplier tubes, which were fed a current alternating at 110.003125 MHz, generating a heterodyning frequency of 3.125 kHz. For each detector, the data were sampled at 50 kHz, and a Fast-Fourier transform was used to determine the intensity and phase delay at the heterodyning frequency. Only the phase data were used during the data analysis. An optical montage was chosen that permitted each detector to pick-up light from up to sixteen sources (i.e., a maximum of sixteen source fibers were located closer than 70 mm to each detector – the maximum theoretical distance for which a measurable amount of photons emitted by a source can be picked up by a detector given the optical properties of the human head). To keep the light coming from each of these sixteen sources separable from one another, they were time-multiplexed – switching them on for 1.6 ms and off for 24 ms. In order to prevent cross-talk, sources and detectors were positioned and illuminated such that no two light sources within the range of one detector were on at the same time, using an automated procedure (Mathewson et al., 2014). This resulted in 384 potential channels per

session. The cycle through each of the 16 multiplexed sets of sources lasted 25.6 ms, with an effective sampling frequency of approximately 39.1 Hz. Sources and detectors were arranged differently for the second session, resulting in a total of 768 potential channels across the two sessions, with the montage used in each session counterbalanced across subject. Recording locations were selected in order to ensure overlapping coverage of our pre-determined ROIs by multiple channels, and were clustered such that their light illuminated occipital, temporal, and parietal areas (see Figure 3).

Although the subject was alone in a recording room while EROS was recorded, the room is not acoustically insulated (so uncontrolled, faint environmental noise may occasionally filter through). In addition, some of the equipment (computers, EROS recording apparatus) has fans that produce a low-level, continuous white noise (less than 20 dB), which was present for the whole duration of the experiment.

2.4.4 Analysis procedures for optical data

2.4.4.1 Pre-processing

Data were preprocessed using in-house software, P-POD (Pre-Processing of Optical Data, MATLAB code). First, channels were eliminated if the source-to-detector distance was less than 1.75 cm or greater than 5.5 cm, because previous research has shown that channels outside this range either do not penetrate the head enough to be sensitive to brain phenomena (source-detector distances < 1.75 cm) or are reached by too few photons and are therefore too noisy to produce useful data (source-detector distances > 5.5 cm; Gratton et al., 2000; 2006). Next, data were corrected for phase wrapping and de-trended to remove low-frequency drifts. The mean phase delay across each block was set to zero, and the phase of the modulated light was converted to light scattering delay in picoseconds (ps; Chiarelli et al., 2013). The variance in the data due to the hemodynamic pulse was removed with a time-warping regression procedure (Gratton & Corballis, 1995). A band-pass filter was used to remove frequencies in the data below 0.01 Hz or above 10 Hz, as data outside this frequency range has been shown to be related to various sources of biological, environmental, and instrumental noise (Maclin, Gratton, & Fabiani, 2003; Chiarelli et al., 2014). The phase data were signal averaged for each subject, channel, and trial type with time locking to the onset of the response probe array. The averaged data was baseline-corrected using the five points (about 100 ms) preceding stimulus onset. Only channels with low noise (standard deviation of phase delay < 200 ps) were included in the

group-level analyses. Finally, a moving-average boxcar filter of three points was applied to the data to reduce high-frequency noise.

2.4.4.2 Co-registration

Following each EROS session, the locations of light sources and detectors were digitized using either a Polaris Vicra camera and Brainsight software, or a Polhemus Fastrak, model 3SF0002. These locations were then co-registered to the structural MR images using fiducials alignment and a surface-fitting Levenberg and Marquard algorithm (Whalen et al., 2008; Chiarelli et al., 2015). Finally, the locations were warped into the Talairach templates (Talairach and Tournoux, 1988) using Statistical Parametric Mapping functions (Penny et al, 2011) and affine transformations (Lancaster et al., 2007). Talairach transformed locations were used for further analysis by the software Opt-3d.

2.4.4.3 Image reconstruction and statistical maps

In-house software “Opt-3d” (Gratton, 2000) was used to combine data from channels whose diffusion paths intersected a given voxel (Wolf et al., 2000) and to compute statistics. Since we were interested in surface reconstruction of the phase data, we used a procedure by which, for each channel, each pixel on the head surface is assigned a weight related to the estimated sensitivity of the measures to phenomena (scattering and absorption changes) occurring in brain regions underlying that pixel. Although this method lacks depth localization, it allows to avoid inverse procedures which inherently decrease the Signal to Noise Ratio of the reconstructed image (Chiarelli et al., 2016). The sensitivity was estimated based on a perturbation model presented by Feng et al, (1995), adapted for phase delay data.

Data were spatially filtered with an 8-mm Gaussian kernel. To compute statistical maps, group-level *t*-statistics were derived across subjects and then converted into *z*-scores, with appropriate correction for multiple comparisons using random field theory (Worsley & Friston, 1995; Kiebel et al., 1999). *Z*-scores were orthogonally projected onto sagittal and coronal surfaces of a brain in Talairach space. These procedures, taken together, control for multiple comparisons across space.

2.4.4.4 ROIs

All ROIs were established on the basis of previous research comparing brain activity in deaf and hearing individuals (Bavelier, et al., 2001; Jola, et al., 2013; Stevenson & James, 2009), using Talairach coordinates (Talairach and Tournoux, 1988). These include early visual cortex (V1-V2),

primary auditory cortex (HG), auditory association areas (posterior BA22), and attentional control areas (PPC).

For all areas except for V1-V2, data from the left and right hemispheres were analyzed separately. All these areas had the same coordinates (established *a priori*) for all individuals, with the exception of HG. HG is (a) quite small, and (b) previous research has shown that its exact coordinates are quite variable across individuals (Abdul-Kareem & Slumming, 2008). Therefore, the ROI was established separately for each subject by locating its center in the Talairach transformed anatomical images. All the ROIs were box-shaped, with coordinates reported in Table 3.

2.4.4.5 Statistical analyses

All statistical tests of EROS data were based on a *t*-test for differences between groups (deaf adult vs. NH control). All were two-tailed tests, with the following exceptions for which we had *a priori* directional hypotheses and therefore used one-tailed tests. We predicted that deaf adults would show greater activation than NH controls in the following ROIs: V1-V2, HG (RH), posterior BA22 (RH).

3. Results

3.1 Perceptual threshold tasks

3.1.1 Central discrimination

Data for one NH control was excluded from this analysis because the participant failed to understand instructions. Once instructions were clarified, however, the participant performed normally on the two subsequent tasks and was therefore included in all subsequent analyses. One deaf adult had a threshold more than 3 standard deviations above the grand mean for all participants, and was therefore excluded from the study. Average thresholds on each task for deaf adults and NH controls are shown in Figure 4. A two-tailed test was used as no differences between groups were expected. Deaf adults ($M = 32.9\text{ms}$) and NH controls ($M = 28.2\text{ms}$) did not significantly differ on the central discrimination task ($t(12) = 0.70$, $p = .496$).

3.1.2 Central discrimination plus peripheral localization

A two-tailed test was used as no differences between groups were expected. Deaf adults ($M = 35.5\text{ms}$) and NH controls ($M = 33.4\text{ms}$) did not significantly differ on this task ($t(19) = 0.48$, $p = .634$).

3.1.3 Main UFOV task

In this task one deaf adult had a central staircase threshold more than 3 standard deviations above the grand mean for all participants, and was therefore excluded from the study. For the central staircase a two-tailed test was used as no differences between groups were expected, but a one-tailed test was applied to the peripheral staircase as a significant decrease in threshold (better performance) was expected for deaf participants. As predicted, in the UFOV task, there was a statistically significant group difference in peripheral localization thresholds ($t(19) = 1.96, p = .033$). The threshold for deaf adults was 162.7ms compared to 262.1ms for NH controls. This result indicates that the deaf adults, on average, needed less presentation time than did NH controls to successfully localize a peripheral visual target in a field of distractors. Importantly, there was no difference in the concurrent central discrimination task ($t(19) = 0.10, p = .923$), indicating that the advantage was not due to a trade-off with central task performance.

3.2 EROS analysis

3.2.1 Behavioral performance during EROS data collection

In order to determine whether or not there were performance differences during optical recording, we computed accuracy (percent correct) for the central and peripheral tasks averaged across the two testing sessions. Tests between groups for central task accuracy were two-tailed. Tests between groups for peripheral accuracy and tests against chance were one-tailed. Two deaf adults were excluded from this behavioral analysis due to equipment malfunction resulting in loss of their behavioral performance data. These subjects were included in subsequent optical analyses as only their behavioral data was missing, not their neuroimaging data.

No statistically significant difference was found between groups for both the central task ($t(14) = 0.08, p = .939$) and the peripheral task ($t(14) = 0.42, p = .339$). Deaf adults had a mean accuracy of 94.5% on the central task ($SD = 4.4\%$) and 55.3% accuracy on the peripheral task ($SD = 20.0\%$). Hearing participants had a mean accuracy of 95.3% on the central task ($SD = 5.9\%$) and 51.9% accuracy on the peripheral task ($SD = 11.8\%$). Thus the performance of the deaf adults and NH controls was comparable. Because the groups did not significantly differ on these measures, they were collapsed into one group and compared to chance. This analysis revealed that subjects were well above chance on both the central task ($t(15) = 34.69, p < 0.001$; chance = 50%) and the peripheral task ($t(15) = 7.35; p < 0.001$, chance = 25%). These results indicate that our choice of presentation duration had the expected effect of equalizing performance across the two groups without inducing floor effects.

An ANOVA with group and task location as factors found a main effect of location ($F(1,14) = 110.24, p < 0.001$) such that the central task resulted in higher accuracy than the peripheral. There was no main effect of group ($F(1,14) = 0.158, p = 0.697$) and no interaction effect ($F(1,14) = 0.167, p = 0.689$). These results reflect the above described t-tests.

3.2.2 Optical data analysis

The dependent measure for optical data analysis was change in photon delay (measured in picoseconds) from the baseline value, averaged over all trials for each subject and condition. Three-dimensional data from voxels are projected onto their respective 2D left and right sagittal and coronal surfaces. We only report here the results of the between-group contrast (deaf adult vs. NH control). In this contrast, positive values reflect an increase in neural activity in deaf adults relative to NH controls, and negative values represent a decrease in neural activity in deaf adults relative to NH controls. Maps of these contrasts at latencies at which these effects were most evident (see statistical analyses below) are shown in Figure 5.

The statistical analysis was based on the set of ROIs described in the Methods section, and identified based on previous research. Data from 39 time points (102.4-1075.2 ms in 25.6 ms bins) were included in the analysis, with 0 as the stimulus onset. The results of the statistical tests for each latency and ROI are presented in Table 4. These data were adjusted for multiple comparisons within each ROI, but not across ROIs or time points. Therefore, they should be considered as exploratory in nature.

Significant effects were observed in four ROIs and at several latencies. Deaf adults showed increased activity (relative to NH controls) in V1-V2 (at four different latencies, ranging between 102.4 and 1075.2 ms) and in the RH posterior BA22 (between 691 ms and 716.8 ms). In most of these cases, simple effect analyses indicated that the effects were due to up-regulations (i.e., values above baseline) for the deaf adults but not for the NH controls (with the exception of some of the late effects in V1-V2 where the effect may be driven by down-regulation in the NH controls). In two ROIs, deaf adults showed less activity than NH controls: LH HG (between 486.4 and 537.6 ms) and LH PPC (between 793.6 and 819.2 ms). Analysis of simple effects suggests that the LH HG difference is due to down-regulation of activity in the deaf adults, whereas the LH PPC effect may be due to up-regulation of activity in NH controls (with respect to baseline).

Taken together, the optical imaging data suggest that deaf adults up-regulate visual cortex activity to a greater extent than NH individuals during the performance of the UFOV task. And, differently from

NH controls, they appear to down-regulate primary auditory cortex during the performance of this difficult visual task. Finally, they appear to recruit secondary auditory regions (i.e., posterior BA 22) in the RH during this task. This final finding aligns with findings from several research groups, and its relationship to behavioral performance was explored further.

3.2.4 Brain-behavior correlations

To determine whether RH recruitment of auditory association areas was related to superior peripheral localization performance, we computed the correlation between the RH posterior BA22 activity (averaged across time points 691.2 and 716.8, which were significant in the ROI analysis) measured in each participant and their threshold on the peripheral component of the UFOV task (which was obtained during a separate session). The results indicated a significant correlation ($r(16) = -0.500$, $p < 0.037$) such that a lower threshold (i.e., better behavioral performance) was correlated with more activity in the RH posterior BA22 ROI (See Figure 6). Those individuals who recruited this region during performance of the UFOV task in the optical imaging session tended to show better performance (i.e., lower threshold) during the behavioral session.

Similar correlations were tested for the four latencies in V1/V2 where differences between groups were found. The correlation for the third peak (896-947ms) approached, but failed to reach, significance ($r(16) = -0.439$, $p < 0.068$). Correlations for the other three peaks were all not significant (all r less than -0.309 , all p less than 0.212).

For the peak in LH PPC (794-819ms), where the deaf had less activity than the hearing, we found a significant correlation with behavior ($r(16) = 0.530$, $p < 0.024$). This positive correlation shows that those individuals who recruited the area more (typically the hearing participants) showed worse performance (see Figure 7).

For the peak in LH HG (486-538ms), where the deaf had less activity than the hearing, we did not find a significant correlation with behavior ($r(16) = 0.357$, $p < 0.146$).

4. Discussion

4.1. Summary of results

4.1.1 Behavioral findings

Our behavioral results replicated previous findings on the visual processing enhancements seen in deaf people (reviewed in Dye & Bavelier, 2013). In particular, behavioral differences between deaf and hearing individuals were only observed for a peripheral task, and then only when there was a

need to select the target from amongst competing visual distractors. This replication of the UFOV was modified in such a way as to magnify the deaf and hearing differences. In the previous study by Dye, Hauser, and Bavelier (2009), the target was a sheriff's badge shape; a filled in star inside of a circle. This target was significantly different from the square distractors not just in that it was a very different shape but also in luminance. We know that peripheral vision is particularly sensitive to luminance due to the increased density of rods over cones in peripheral vision (Jonas, Schneider, & Naumann, 1992). Therefore, it is possible that significant differences in luminance between the target and distractors is what made that version of the UFOV easier, resulting in much lower thresholds for the peripheral task among distractors than observed here (despite the fact that Dye et al. (2009) included twice as many distractors). It is also possible that the target-distractor luminance difference aided the hearing participants in approaching the performance levels of the deaf participants, as we know that deaf and hearing individuals do not differ on more basic sensory tasks (Bosworth & Dobkins, 1999; Bosworth & Dobkins, 2002a; Brozinsky, & Bavelier, 2004; Finney & Dobkins, 2000). Therefore, by using a diamond target embedded amongst square distractors, and eliminating this luminance difference between the target and distractors, we may have honed in on what is truly different between deaf and hearing vision: the ability to localize a target among distractors in the periphery.

However, the large overall increase in the magnitude of the thresholds (compared to Dye et al., 2009) did affect our expectations for the results of behavioral testing during the optical recording. Because the optical recording required a fixed presentation time for all participants, we chose 68 ms as being the most likely in-between point of the deaf and hearing thresholds based on the thresholds obtained in Dye et al.'s study. Our goal was to pick a presentation time that would not bring about large deaf-hearing discrepancies in the behavioral performance of our participants during imaging. The 68 ms presentation time turned out to be well below the average thresholds for the deaf and the hearing participants, making it a difficult task for both groups. Nevertheless, both groups performed well on the central task, and were still well above chance level on the peripheral task.

4.1.2 Optical results

The deaf-hearing differences in early visual cortex are of interest because they may be indicators of unimodal plasticity, such that deaf subjects are using the area differently than the hearing individuals for the same visual task. Evidence of unimodal plasticity in the deaf is much weaker than that of cross-modal plasticity. For example, while Neville, et al. (1983) found increased P230 amplitudes for deaf over hearing participants in occipital areas, Chlubnová, et al. (2005) found a decrease in

amplitude of visual evoked potentials in the deaf participants relative to the hearing, and no changes in its latency. Bottari, et al. (2011) presented deaf and hearing subjects with visual stimuli and found that in deaf subjects the P1 contained two peaks as opposed to just one in the hearing, and had a higher amplitude around 100ms. However, EEG techniques have lower spatial resolutions relative to MEG and fMRI (Fabiani, et al., 2007). Therefore, determining if these changes in the ERP signal occurred in primary visual areas without applying source modeling algorithms may be difficult. Fine et al. (2005) found no changes between the deaf and hearing in early visual areas in an MRI study. The finding presented here needs to be replicated, and techniques like EROS, which provide both the spatial resolution to localize the signal to early visual cortex and the temporal resolution to ensure the signal is in fact representative of early processing and not later feedback mechanisms, represent a uniquely useful way of examining this question.

We observed EROS effects distinguishing deaf from hearing subjects in V1/V2 at the following latency intervals: 102-154 ms, 435-537 ms, 896-947 ms, and 1075ms. The first of these intervals overlaps with previous ERP findings (e.g., Bottari et al., 2011; 2014).

Event-related neural activity in posterior BA22 in the RH for the deaf adults was both significantly above baseline and greater than that observed in the normal-hearing controls. This successfully replicates previous findings in the literature that secondary auditory areas, particularly in the posterior regions of temporal cortex, show more activation for the deaf than the hearing in purely visual tasks (Bavelier, Dye, & Hauser, 2006). Interestingly, the analysis of data obtained from LH HG indicated that the deaf, but not the hearing individuals, down-regulated this region while processing visual stimuli. While this may have been predicted for NH controls, it was an unexpected finding in the deaf participants.

The findings in LH PPC indicate increased activity in hearing controls compared to the deaf adults. One possible interpretation of this is that hearing subjects, who struggle more with the task outside the scanner, require stronger activation of their attentional control to complete the task. The PPC has been implicated in the orienting of visual attention in humans (e.g. Corbetta, et al. 2000; for a review see Kastner & Ungerleider, 2000). Such an explanation might also suggest differences in attention control strategies between the two groups that could arise from the potential distraction that hearing individuals might experience due to environmental noise – which would not be an issue for deaf individuals. While blindfolding of normally-sighted controls is increasingly common in the blindness

literature, those working on human deafness have yet to adopt agreed-upon practices for the temporary attenuation of auditory experience in NH control subjects.

The results of the study point to two types of phenomena that may differ between the deaf and hearing groups. The first is enhanced responses in early visual areas, beginning at around 100-150 ms, but also observable at longer latencies, with larger effects in V1/V2 for the deaf compared to the hearing subjects. The early interval corresponds in time with the early visual evoked potential effects observed by other investigators. Modulation of the amplitude of early VEPs is often interpreted as due to attention effects. Based on the bias-competition hypothesis (Desimone & Duncan, 1995), we may hypothesize that deaf people are better able to suppress competition between visual representations in peripheral vision than normally hearing adults, resulting in stronger activity levels. This may derive from increased peripheral acuity, perhaps accumulated over extensive use. Alternatively, it may reflect reduced competition from auditory stimulation, resulting in more efficient preparatory states (this could be evaluated using paradigms allowing us to assess these putative preparatory processes). The subsequent activities in this region may represent re-entry or feedback phenomena. The second set of phenomena reflects enhanced processing in the deaf people in areas not normally used for visual processing, such as the right BA 22. This may reflect enhanced recruitment in this area, perhaps due to a lack of competition from auditory input. In our deaf population, this lack of competition is chronic (i.e., it is present since birth or early childhood) and may have led to substantial re-wiring of the area. This may reflect a “use-it-or-loose-it” process supporting structural connectivity. This interpretation is supported by data indicating white matter differences in the posterior STG in deaf compared to hearing individuals (Shibata, 2007; Li, et al., 2012), as well as reduced connectivity within auditory regions but increased connectivity between visual and auditory regions in deaf children (Li, et al., 2015). It is not completely clear how activity in these areas could be beneficial for performance, as it appears to follow, rather than precede the subjects’ responses. Perhaps the benefits reflect some attentional phenomena, such as the ability to maintain visual stimulus or goal representations across trials.”

4.1.3 Brain-and-behavior correlations

We report a significant correlation between brain activity in posterior BA22 of the RH and behavioral thresholds obtained from the peripheral component of the UFOV task. To our knowledge, this is among the first demonstrations of brain-behavior correlations in deafness research (see also Lomber et al., 2011; Bottari et al., 2011; Codina et al., 2011). Potentially, findings of this type may help determine whether the recruitment of auditory processing regions during visual tasks in deaf

individuals is actually related to better performance. A more conclusive statement might be obtained by temporarily inhibiting these regions, for instance using repetitive TMS. Such an approach can benefit from the concurrent temporal and spatial resolution provided by the EROS approach. It is important to note that the brain-behavior correlation reported here was obtained between data collected during different sessions during which participants were performing subtly different tasks. On the one hand, it would be useful to show such a correlation during the same task. On the other hand, the present results, if replicated in future research, may indicate that the plasticity phenomenon is relatively robust across different task levels.

The correlation with LH PPC was not expected and may support our assertion that hearing participants who are struggling more with the task are recruiting attentional control to improve their performance.

4.2. Limitations

4.2.1 Methodological issues

The current study used a novel technique, EROS, for analyzing brain activity during the UFOV task in deaf adults and NH controls. EROS can provide data with high temporal and spatial resolution that can inform us about the dynamics of brain activation, revealing the complex interactions occurring between different brain areas during complex tasks such as the UFOV. It can also reveal how these complex interactions are altered in the absence of particular sensory inputs, such as occurs in deaf, blind, and deaf-blind individuals. The data presented in this paper present a glimpse at such a possibility. However, there are two major caveats to the current study. First, the sample sizes for each of the two groups are small, and EROS, at least in its present form, possesses a limited signal-to-noise ratio. Both of these factors severely limit the statistical power of the study. One consequence of this is that we could not completely correct for multiple comparisons in our analyses. As such, the results are exploratory and further replications are needed. Within this context, the correlation observed between brain activity and behavioral performance (which was obtained in a separate session) is encouraging, but caution is required.

A second methodological issue is the suggestion, coming from the brain activation data, that the difference between deaf and hearing individuals might not be due solely to long-term plasticity induced by the lack of auditory input in the deaf participants, but also by strategic adjustments required by the need to suppress auditory noise in the NH controls (although care was taken to minimize noise during EROS data collection). This possibility could be explicitly addressed by

experimentally controlling the level of auditory noise present during the task – perhaps a need for any experiment investigating differences in visual abilities between deaf and hearing individuals.

4.2.2 Theoretical implications

Taken at face value, the data presented here suggest that a complex set of phenomena is implicated in the processing of peripheral visual stimuli (such as in the UFOV task), with both “visual” and “auditory” areas participating in different ways in deaf adults and NH controls. Deaf individuals showed increased activation of visual areas, less activation of primary auditory cortex, and recruitment of an area, RH posterior BA22, which is typically involved in auditory processing.

4.3 Conclusion

While low participant numbers, high amounts of noise inherent to optical recording, and the exploratory nature of this project all limit interpretation of the data, this is to some extent true of neuroimaging work with any relatively low-incidence population. The percent of adults in Illinois with any hearing loss is approximately 1.6% (Harrington, 2014), and the percent of those meeting our criteria of severe to profoundly deaf starting before age 5 will be even lower. Given the many advantages of using EROS in studying populations with hearing loss, this study can be considered proof of concept: differences between deaf and hearing adults typically found with other imaging modalities can be replicated with EROS. This is particularly important given the utility of the technique for use with children, and people with cochlear implants. In these groups CT scans or template brains could be used for alignment, avoiding the issues associated with sMRI administration in these populations. Studying brain development in both of these groups could give unique insights into the ways that sensory experiences contribute to the complex and dynamic networks that support cognition. Future work can leverage the analyses conducted here to guide more precise definition of ROIs, IOIs, and network models.

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Table 1. Further information about deaf participants

Participant Code	Age of deafness	Number of deaf parents	ASL fluent?	PTA HL	Age at test
D01	3 years	2	Yes	86.6	29
D02	Birth	2	Yes	100	23
D03	Birth	2	Yes	98	18
D04	Birth	2	Yes	---	27
D05	Birth	2	Yes	106.6	45
D06	Birth	2	Yes	108.3	47
D07	Birth	1	Yes	110	32
D08	1 year	--- ^a	Yes	96.6	32
D09	2 years	--- ^a	Yes	96.6	47
D10	Birth	0	No ^b	110	47

^a Participant indicated deaf relatives, but did not specify exact relationship.

^b Participant communicated with the experimenter solely in ASL throughout the experiment, and did not appear to struggle with comprehension.

Table 2. Subject inclusions and exclusions throughout the study. Task 1 refers to the central-only task. Task 3a refers to the central task thresholds when distractors were present.

	generally eligible for all tests	included in audiology	Included in behavioral central task (control)	Included in behavioral dual task (control)	Included in behavioral distractors task (experimental)	included in EROS
D1	yes	yes	yes	yes	yes	yes
D2	yes	yes	yes	yes	yes	yes
D3	yes	yes	yes	yes	yes	yes
D4	yes	no, self-reported	yes	yes	yes	yes
D5	yes	yes	yes	yes	yes	no, data loss from equipment malfunction
D6	yes	yes	yes	yes	yes	yes
D7	yes	yes	yes	yes	yes	yes
D8	yes	yes	yes	yes	yes	yes
D9	yes	yes	yes	yes	yes	yes
D10	yes	yes	yes	yes	yes	yes
D11	no, poor central task thresholds in task 1	no	no	no	no	no
D12	no, poor central task thresholds in task 3a	no	no	no	no	no
D13	no, data loss from equipment malfunction	no	no	no	no	no
H1	yes	yes	yes	yes	yes	yes
H2	yes	yes	yes	yes	yes	yes
H3	yes	yes	yes	yes	yes	yes
H4	yes	yes	yes	yes	yes	yes
H5	yes	yes	yes	yes	yes	yes
H6	yes	yes	yes	yes	yes	yes
H7	yes	yes	yes	yes	yes	yes
H8	yes	yes	yes	yes	yes	yes
H9	yes	yes	yes	yes	yes	yes
H10	yes	yes	yes	yes	yes	no, subject fell ill
H11	yes	yes	no, subject misunderstood instructions	yes	yes	no, data loss from equipment malfunction

Table 3. Limits of box-shaped ROIs used in the study for the analysis of EROS data (all reported in Talairach space). For HG, the coordinates shown are averages across participants.

ROI	x	y	z	size
V1-V2 (both hemispheres)	-22, 22	-98, -74	-14, 18	33.792cm ³
Lingual Gyrus (LH)	-33, -13	-85, -65	-13, 7	8cm ³
Lingual Gyrus (RH)	6, 26	-82, -62	-13, 7	8cm ³
HG (LH)	-57, -37	-29, -9	1, 21	8cm ³
HG (RH)	38, 58	-25, -5	1, 21	8cm ³
Posterior BA22 (LH)	-71, -37	-62, -29	1, 21	22.44cm ³
Posterior BA22 (RH)	37, 71	-62, -29	1, 21	22.44cm ³
PPC (LH)	-46, -26	-50, -30	42, 62	8cm ³
PPC (RH)	22, 42	-66, -46	42, 62	8cm ³

Table 4. EROS results: t-statistics for deaf vs. NH control comparisons in key ROIs at all time intervals. Positive values represent deaf > NH control; negative values indicate NH controls < deaf.

Time	V1-V2	HG LH	HG RH	BA22 LH	BA22 RH	PPC LH	PPC RH
102.4	1.892*	0.795	-0.611	-0.663	-0.183	-0.556	-0.734
128	2.025*	-0.006	-0.935	-1.196	0.337	-0.304	-0.541
153.6	1.772*	-0.319	-0.433	-1.551	0.182	0.162	-0.256
179.2	1.106	0.423	0.780	-0.615	-0.092	0.138	-0.273
204.8	0.557	1.089	1.186	-0.016	-0.089	-0.238	-0.378
230.4	0.573	0.932	0.352	-0.134	0.130	-0.662	0.029
256	1.141	0.516	-0.378	-0.489	0.420	-1.171	0.949
281.6	1.477	0.314	-0.344	-0.506	0.806	-1.279	1.434
307.2	0.754	0.141	0.497	0.190	0.898	-1.286	0.816
332.8	-0.254	-0.493	0.629	0.607	0.571	-0.907	-0.483
358.4	-0.667	-0.964	0.421	0.338	0.456	0.053	-1.031
384	-0.146	-0.794	0.119	0.131	0.443	0.367	-1.045
409.6	1.258	-0.536	-0.428	0.413	0.379	0.276	-0.691
435.2	2.036*	-0.607	-1.247	0.385	-0.010	-0.270	-0.157
460.8	1.992*	-1.843	-1.809	-0.912	-0.527	-1.269	0.314
486.4	1.801*	-2.933**	-2.023	-1.408	-0.790	-1.166	0.407
512	2.018*	-2.941**	-1.733	-0.936	-0.640	-0.477	0.088
537.6	2.051*	-3.128**	-1.184	0.019	0.386	-0.290	-0.212
563.2	1.745	0.168	-0.675	0.095	1.379	-0.633	0.043
588.8	1.183	1.149	-0.585	-0.626	1.058	-0.698	0.569
614.4	0.475	0.594	-0.811	-0.879	0.434	-0.254	0.336
640	0.505	-0.988	-1.028	-0.268	0.510	-0.291	-0.148
665.6	1.465	-0.727	-0.956	0.704	1.521	-0.837	-0.221
691.2	1.610	-0.081	-0.874	0.587	2.100*	-1.107	-0.111
716.8	1.440	0.272	-0.694	-0.740	2.177*	-0.653	0.133
742.4	0.871	0.095	0.201	-1.325	1.499	-0.557	0.256
768	0.983	-0.352	0.632	-1.572	0.661	-1.652	0.187
793.6	1.005	-0.416	0.445	-1.372	0.238	-2.621* ^a	-0.204
819.2	0.451	-0.115	0.354	-0.914	-0.059	-2.972* ^a	-0.797
844.8	0.189	-0.041	0.530	0.411	-0.286	-1.989	-0.756
870.4	1.237	-0.124	0.796	0.816	0.073	-0.723	-0.456
896	2.345*	-0.425	0.363	0.423	0.947	-0.478	0.074
921.6	2.528*	-0.974	-0.255	-0.388	1.236	-0.811	0.740

947.2	1.812*	-0.895	-0.062	-0.842	1.648	-1.240	0.247
972.8	1.008	0.153	0.821	-0.204	1.182	-1.487	-0.721
998.4	0.824	0.541	0.911	0.645	1.023	-1.333	-1.015
1024	1.234	0.371	0.136	0.530	0.842	-1.063	-1.088
1049.6	1.719	-0.265	-0.766	0.048	0.070	-1.028	-0.881
1075.2	1.890*	-0.876	-1.213	-0.198	-0.422	-1.001	-0.419

* $p < .05$; ** $p < .01$, ^a $df = 9$ (all other $df = 16$)

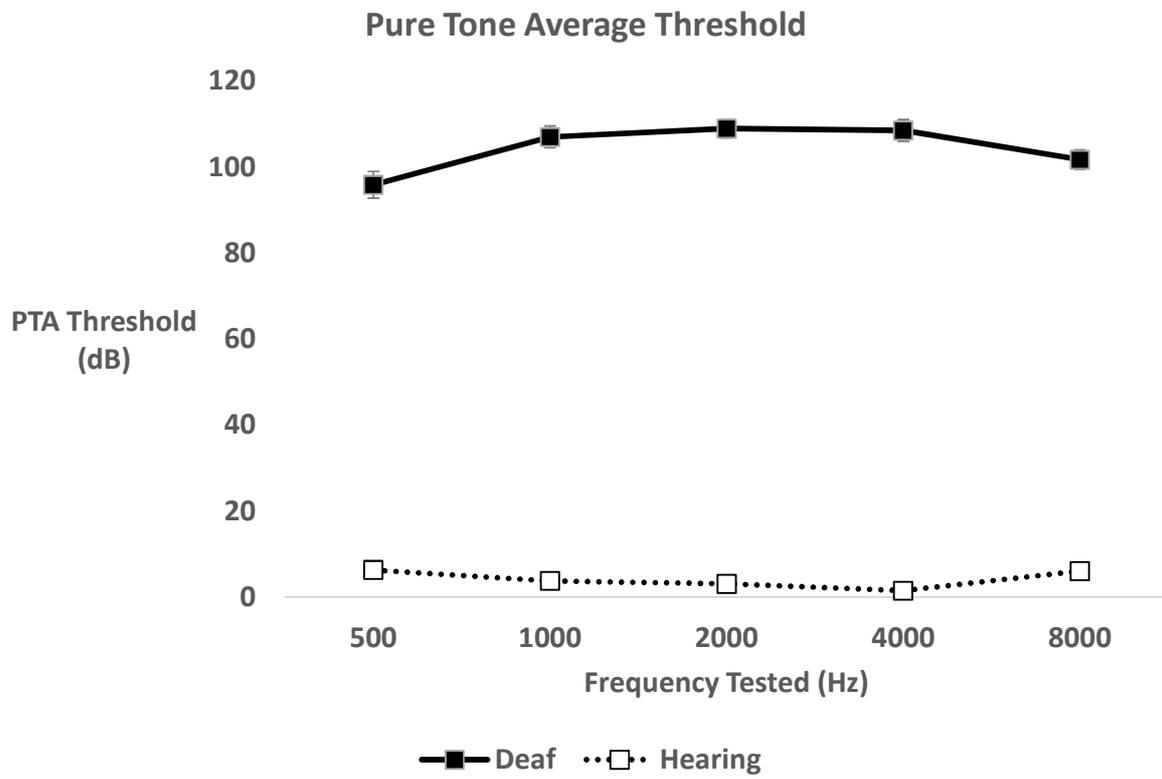


Figure 1

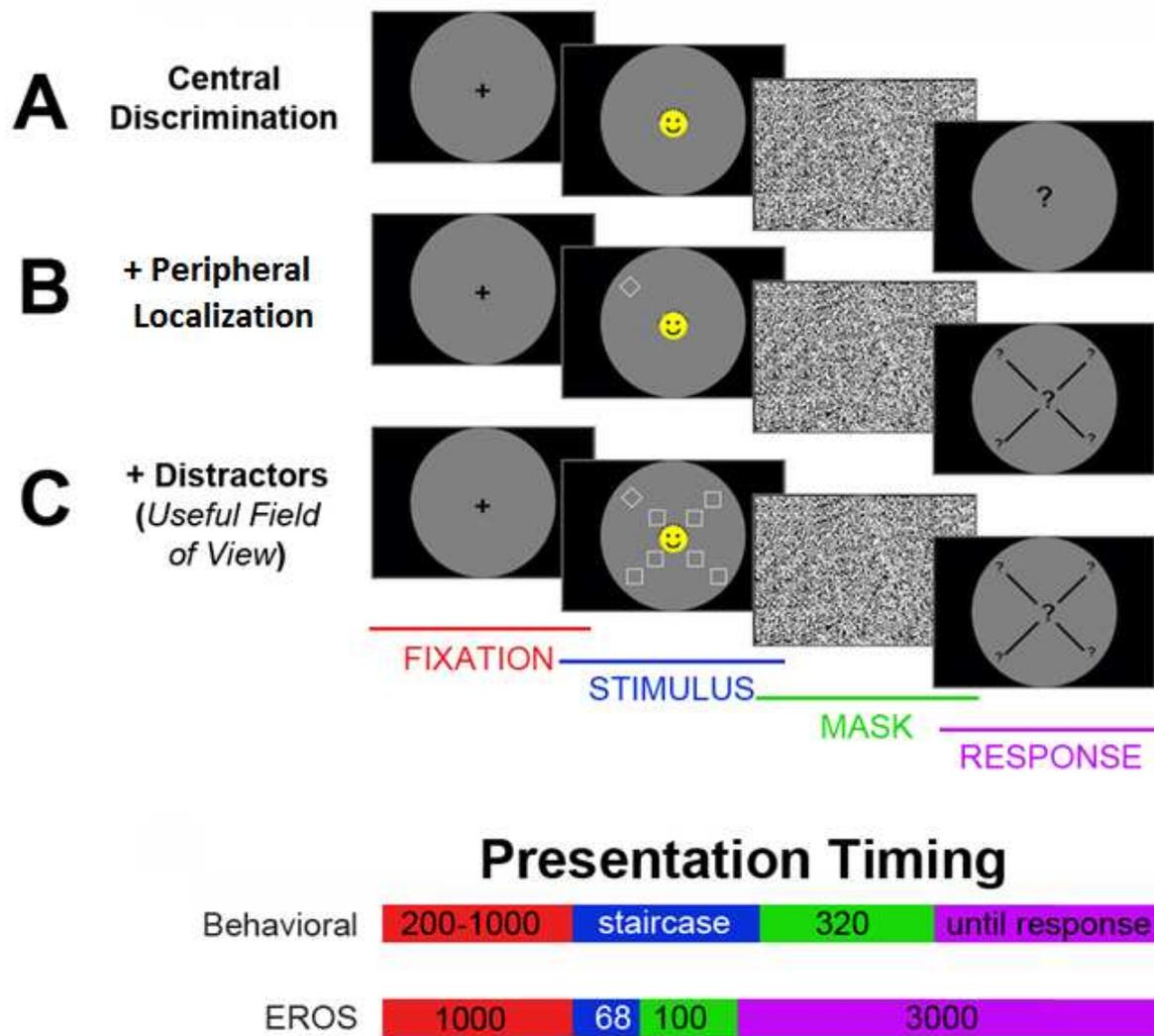


Figure 2

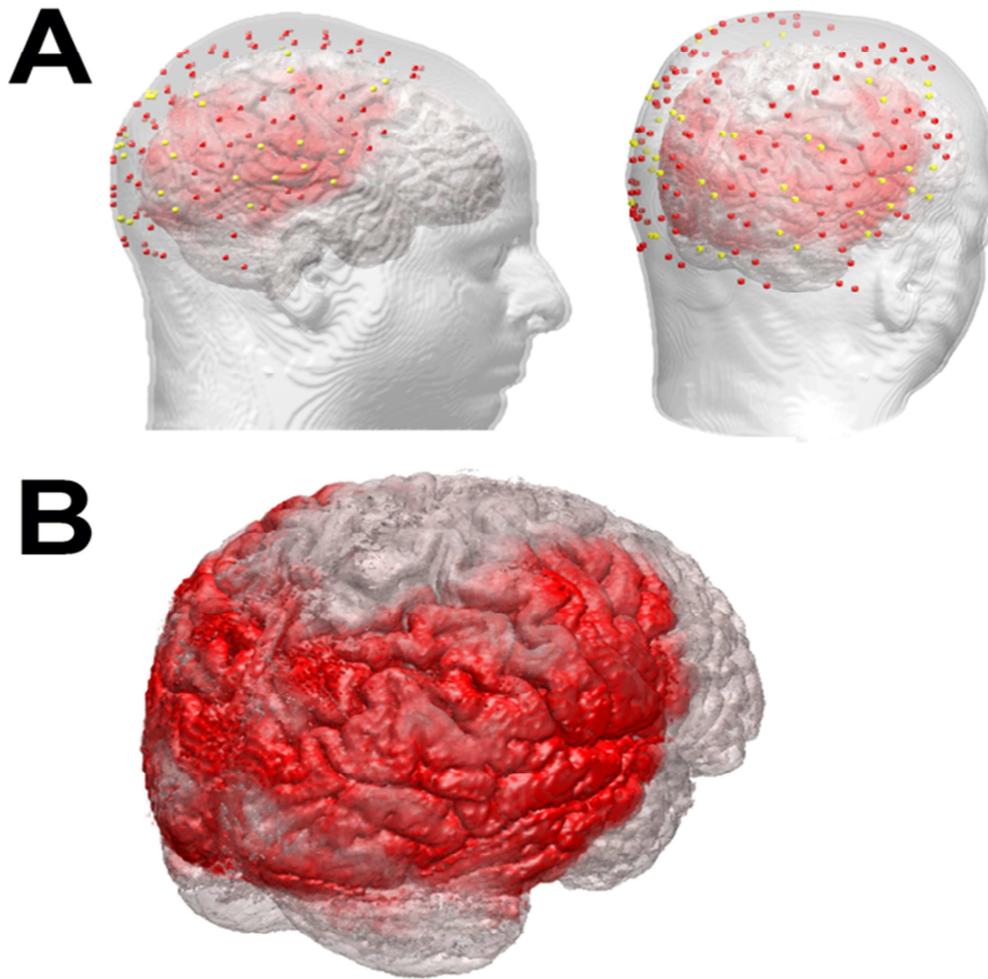


Figure 3

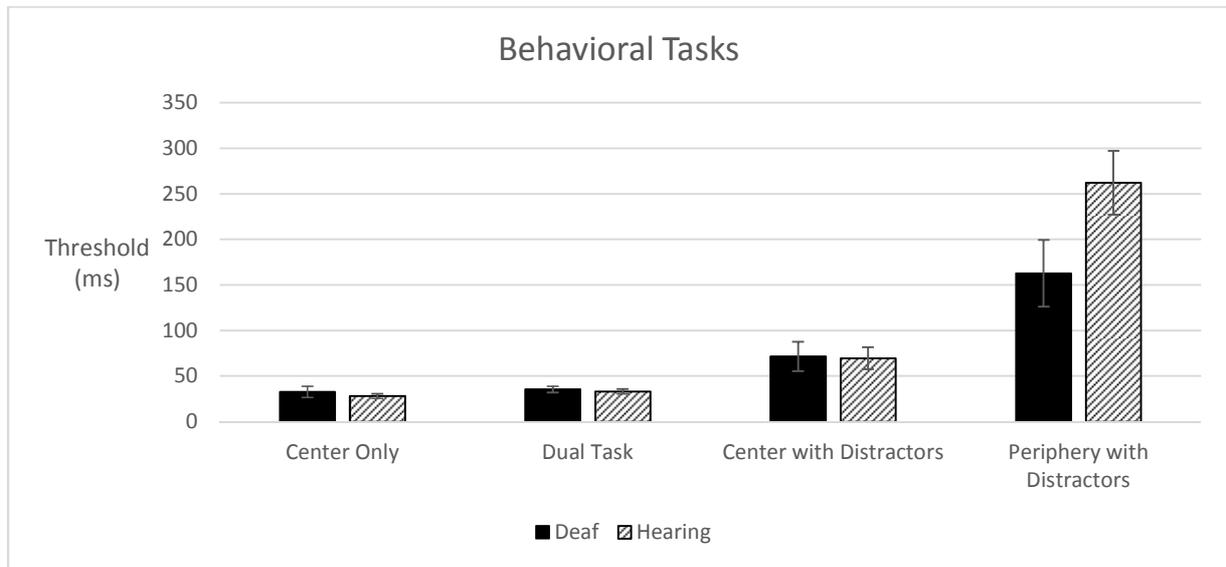


Figure 4

EROS data: Deaf adult – NH control contrast

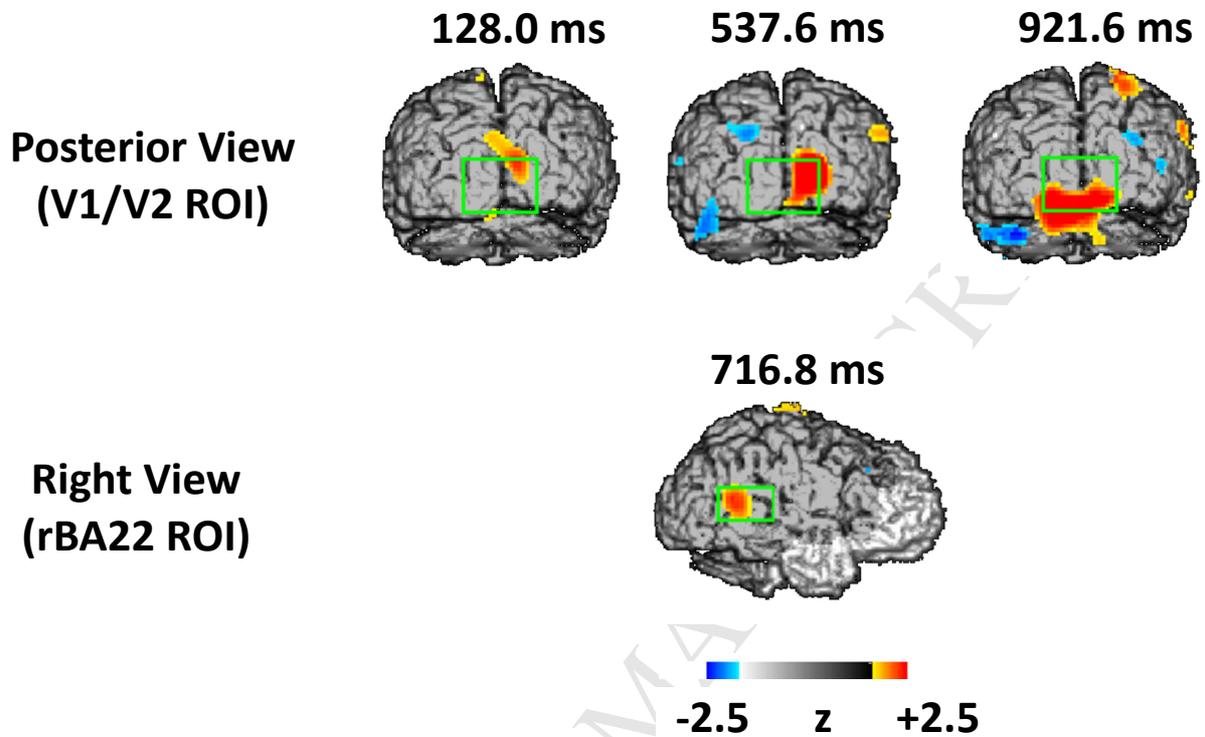


Figure 5

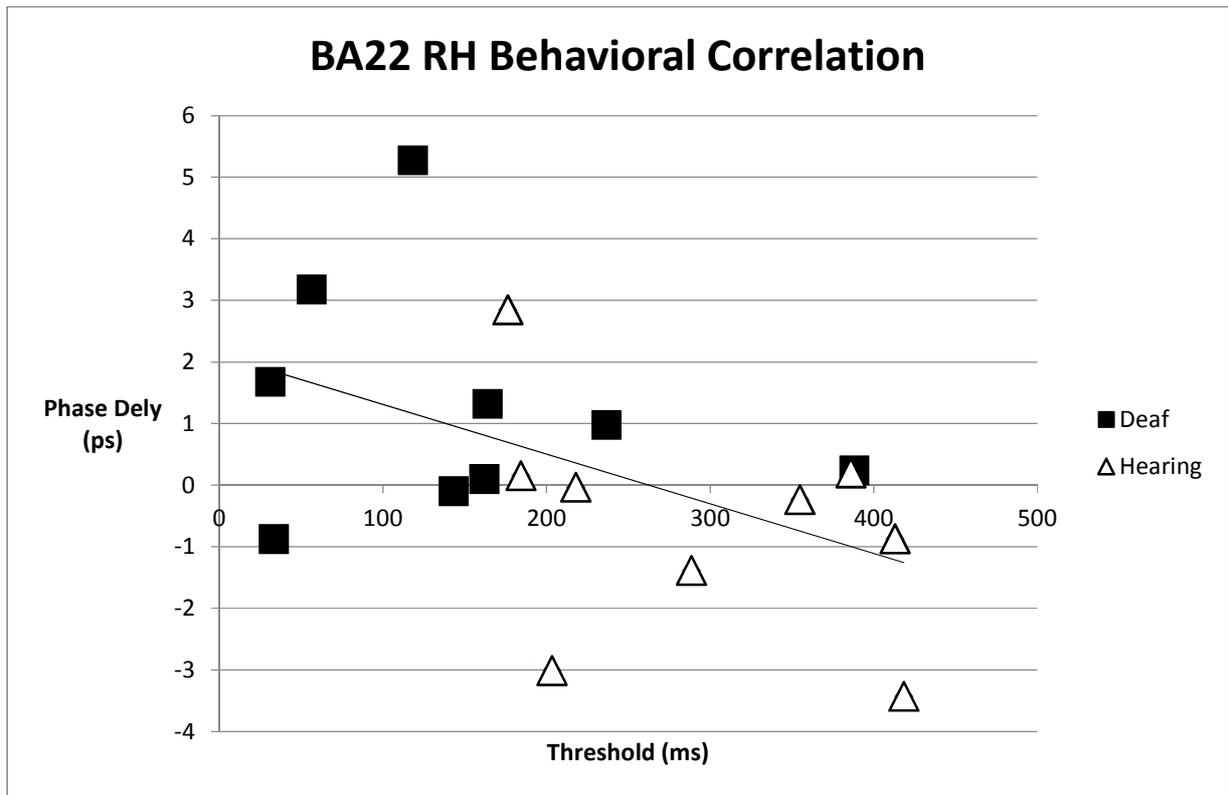


Figure 6

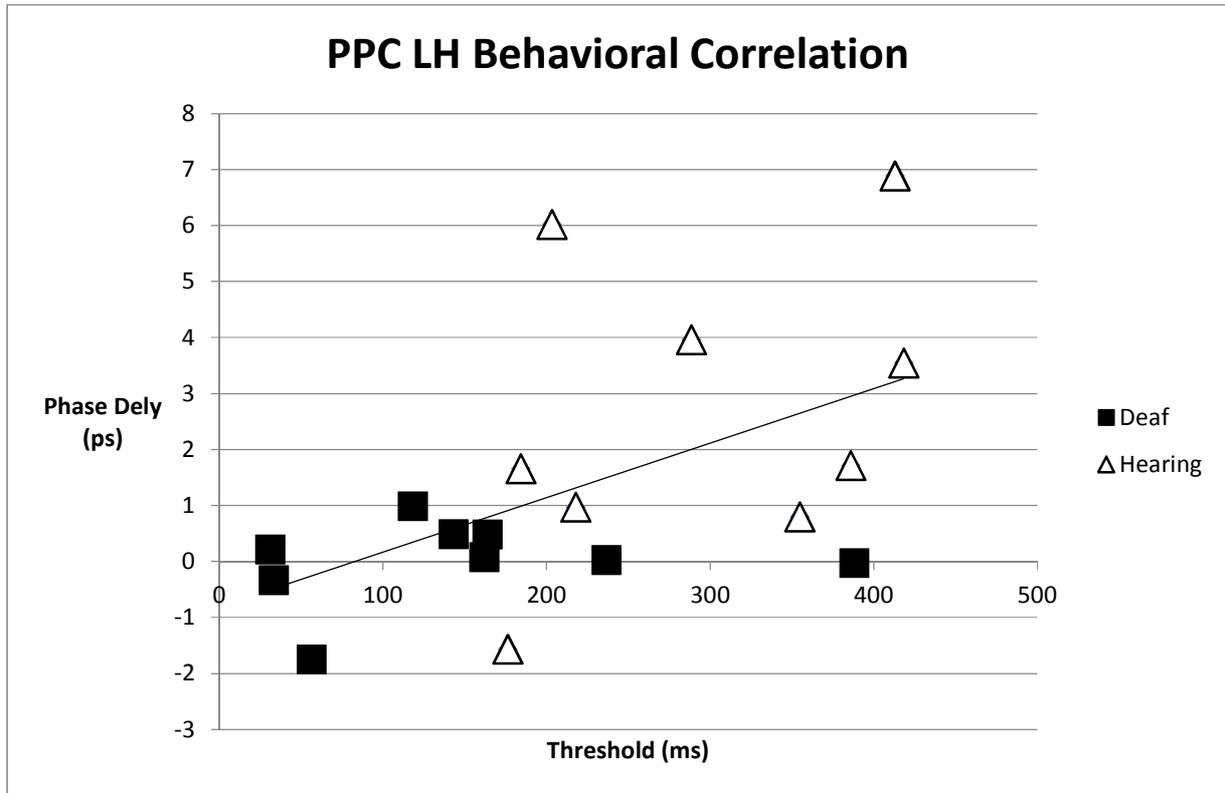


Figure 7

Figure Legends

Figure 1. Group audiograms showing mean and SEM of dB hearing loss across five tested frequencies for deaf adults and NH controls. Thresholds were averaged across the right and left ears for each frequency. Please note that error bars are present for all data points but in many cases are too small to be visible.

Figure 2. Diagrammatic representation of a single Useful Field of View trial. After an initial fixation period (the onset of which forms the baseline for optical data analysis), a visual stimulus was presented, followed by a full-field white noise mask, and then a response screen. Task A required a difficult discrimination of a central target (emoticon face) presented at fixation. Task B added an additional requirement – peripheral localization of a target presented at 20 degrees of visual angle. Finally, Task C – the Useful Field of View task proper – asked participants to perform Task B in the presence of visual distractors. An adaptive staircase procedure was used for behavioral testing outside of the optical imaging lab, whereas the presentation timing parameters were fixed for optical imaging (presentation timing parameters are indicated in ms).

Figure 3. A. Location of optical sources (red dots) and detectors (yellow dots) co-registered with the scalp from a structural MR of a single participant, along with the participant's brain shaded with the density of EROS coverage. B. Different montages were used in the two imaging sessions, resulting in the coverage map shown here. Red areas on the brain indicate voxels that intersected with the flight path of the IR light (shaded by number of overlapping channels) and from which the EROS signal could be recorded (appropriate source to detector distance). The montages were selected to maximize coverage of occipital and temporal regions, with sparse or no coverage of superior parietal and frontal areas. Note that this coverage map would be different for each individual based on differences in anatomy and optode placement.

Figure 4. Graph showing the behavioral performance of deaf and NH control subjects across the behavioral tasks. Thresholds in ms are reported, so recall that lower thresholds equate to better performance. Standard error for each group is shown in the error bars.

Figure 5. Top Row: Posterior view of difference in EROS activity after UFOV stimulation between deaf adults and NH controls at some selected latencies. The green box indicates the V1-V2 ROI. Values in red indicate greater EROS activity for deaf adults compared to NH controls. Bottom Row: Right lateral view of difference in EROS activity after UFOV stimulation between deaf adults and NH controls at one selected latency. The green box indicates the RH posterior BA 22 ROI. Again, values in red indicate greater EROS activity for deaf adults compared to NH controls.

Figure 6. Graph depicts the correlation between behavioral performance (thresholds) and the activity in BA22 RH (phase delay) for each subject. Activity for each subjects was averaged over the two time points which showed significant difference between deaf and hearing participants. Deaf participants are represented in orange and hearing participants are represented in blue.

Figure 7. Graph depicts the correlation between behavioral performance (thresholds) and the activity in PPC LH (phase delay) for each subject. Activity for each subjects was averaged over

the two time points which showed significant difference between deaf and hearing participants. Deaf participants are represented in orange and hearing participants are represented in blue.

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- Replicated findings that deaf subjects require lower presentation thresholds to accurately perform a peripheral visual localization task, relative to normal-hearing controls
- Found evidence for uni-modal plasticity in deaf subjects, with higher activation of a V1/V2 ROI in deaf subjects relative to normal-hearing controls.
- Found evidence for cross-modal plasticity in deaf subjects, with higher activation of a posterior BA22 ROI in the right hemisphere only in deaf subjects relative to normal-hearing controls
- Improved behavioral performance on the visual localization task is predicted by cross-modal activation of auditory association areas