

Running head: Visual performance in congenital deafness

TITLE

Compensatory plasticity in the congenitally deaf for visual tasks is restricted to the horizontal plane.

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### **Abstract**

Congenitally deaf individuals, when compared to hearing individuals, typically show differential performance (improvements or impairments) on certain non-auditory tasks. Concomitantly, their auditory cortex is recruited to process information from the spared senses. Are these compensatory behavioral strategies equally observable across the sensory fields of each particular unaffected sense (e.g., across the full visual field for vision-related compensatory plasticity)? There are neural data in human and non-human mammals that may be suggestive of there being a differential processing advantage for stimuli presented in the horizontal visual plane than in the vertical visual plane. To test for these visual field asymmetries in compensatory behavioral performance, we used a direction of motion discrimination task, and found that deaf participants were better at determining the direction of motion of dot patterns presented in the horizontal plane, when compared to those presented in the vertical plane and in the center – i.e., we show that the neuroplasticity-induced bias towards the horizontal plane is also present in the behavioral advantage that deaf individuals present. These data may suggest that the neuroplastically changed auditory cortex of deaf individuals is functionally responsible for the enhanced processing of information from the spared senses.

**Keywords:** Congenital Deafness; Compensatory Plasticity; Neuroplasticity; Direction-of-Motion Discrimination

## Introduction

The brain of individuals that are congenitally deprived of a sense can undergo considerable plasticity. In these individuals, the deafferented sensory cortex suffers massive neuroplastic changes throughout ontogeny, in the context of a normally developing brain. Because of this, sensorial congenital deprivation has been a major model for our understanding of long-term neuroplasticity. Interestingly, it has been reported that individuals that are congenitally deprived of a sense present differential performance in particular tasks. For instance, these individuals may develop strategies and abilities that lead to superior performance in certain tasks over stimuli presented to the unaffected senses (e.g., Amaral & Almeida, 2015; Bavelier, Dye, & Hauser, 2006; Bavelier & Hirshorn, 2010; Bavelier & Neville, 2002; Merabet & Pascual-Leone, 2010), and at the same time show impoverished performance on other tasks (e.g., Barker, Quittner, Fink, Eisenberg, Tobey, et al., 2009; Boutla, Supalla, Newport, & Bavelier, 2004; Gheysen, Loots, & Van Waelvelde, 2008; Horn, Davis, Pisoni, & Miyamoto, 2005; Horn, Pisoni, & Miyamoto, 2006; Kral & Eggermont, 2007; Kral, Hartmann, Tillein, Heid, & Klinke, 2002; Parasnis, Samar, Bettger, & Sathe, 1996; Rothpletz, Ashmead, & Thorpe, 2003; Wallace & Corballis, 1973). But are these compensatory strategies and abilities equally observable across the sensory fields of each particular unaffected sense (e.g., across the full visual field for vision-related compensatory plasticity)? That is, is there a general benefit for the processing of sensory information at all locations in the sensory field? Here we address this issue by exploring whether and how the behavioral performance of congenitally deaf humans on visual tasks is dictated by the location of the visual stimulus to be processed in the visual field.

Neural and behavioral plastic changes have been extensively reported in congenitally deaf humans. It has been shown that putative auditory cortex in congenitally deaf humans responds to non-auditory stimulation (e.g., Almeida, He, Chen, Mahon, Zhang, et al., 2015; Finney, Fine, & Dobkins, 2001; Karns, Dow, & Neville, 2012; Levanen, Jousmaki, & Hari, 1998; Lyness, Alvarez, Sereno, & MacSweeney, 2014; Nishimura et al., 1999; but see Hickok et al., 1997). For instance, Finney and colleagues showed that the auditory cortex of congenitally deaf, but not of hearing humans, responds to simple visual stimulation (Finney et al., 2001). Moreover, auditory and visual subcortical regions also show neuroplastic changes in congenitally deaf individuals (e.g., Amaral et al., 2016). Comparative

work has shown very similar results. The auditory cortex of congenitally deaf animals is co-opted to process visual (and somatosensory) stimuli (e.g., Hunt et al., 2006; Meredith & Lomber, 2011; Rebillard et al., 1977, 1980; but see Kral, Schröder, Klinke, & Engel, 2003).

Importantly, these changes have also been clearly demonstrated in the behavioral performance of deaf individuals. For instance, deaf individuals are better at processing emotional faces than hearing individuals (Arnold & Murray, 1998; McCullough & Emmorey, 1997; but see Fengler, Nava, Villwock, Büchner, Lenarz, et al., 2017), detecting visual stimuli presented in the visual periphery (e.g., Buckley, Port, & Pascalis, 2011; Chen, Zhang, & Zhou, 2006; Neville & Lawson, 1987; Reynolds, 1993; Stevens & Neville, 2006; note that while this is effectively an instance of better performance of deaf individuals over hearing individuals, it may actually be detrimental when trying to discount irrelevant visual distractors), discriminating and detecting visual motion (e.g., Bavelier et al., 2000; Bosworth & Dobkins, 2002a; Bosworth & Dobkins, 2002b; Neville & Lawson, 1987), and demonstrate heightened tactile sensitivity (Levanen & Hamdorf, 2001). There are, however, many non-auditory tasks in which deaf and hearing individuals perform similarly – e.g., both groups present similar contrast sensitivity thresholds (e.g., Finney & Dobkins, 2001) – and tasks in which deaf individuals are outperformed by hearing individuals (e.g., Barker et al., 2009; Boutla et al., 2004; Gheysen et al., 2008; Horn et al., 2005; Horn et al., 2006; Kral & Eggermont, 2007; Kral et al., 2002; Parasnis et al., 1996; Rothpletz et al., 2003; Wallace & Corballis, 1973). Specifically, it has been shown that deaf individuals show deficits in tasks that depend heavily on sustained visual attention (e.g., Barker et al., 2009; Kral & Eggermont, 2007; Rothpletz et al., 2003), on fine motor control and coordination (e.g., Gheysen et al., 2008; Horn et al., 2006), and, for instance, on verbal working memory (e.g., Boutla et al., 2004; Parasnis et al., 1996; Wallace & Corballis, 1973). Interestingly, the use of auditory neuroprosthetic devices, such as cochlear implants (CI), may ameliorate some, but not all, of these issues, even after early CI implantation. For instance, Yuce and Derim (2008) showed that while deaf children implanted early (before their third birthday) presented better results on visual attention tasks than late implanted children, visual attention skills of both early and late implanted deaf children were impaired when compared to hearing children (see also e.g., Campbell & Sharma, 2016; Conway, Karpicke, Anaya, Henning, Kronenberger, et al., 2011; Fallon, Irvine, & Shepherd, 2008; Horn et al., 2005; Kral &

Sharma, 2012; Sharma, Nash, & Dorman, 2009). This suggests that some of these compensatory changes are not just due to lack of auditory stimulation, but may be dependent on neuroplastic changes across the auditory system of deaf individuals.

But is this behavioral compensatory plasticity present across the full visual field? As described above, congenitally deaf humans seem to show a behavioral advantage for stimuli presented in the periphery (e.g., Buckley et al., 2011; Chen et al., 2006; Neville & Lawson, 1987; Reynolds, 1993; Stevens & Neville, 2006). Importantly, this advantage has presumably been tied to a heightened ability to allocate attention to peripheral visual locations (e.g., Bavelier et al., 2000). Interestingly, orienting of visual attention by sound cues in hearing individuals relies heavily on interaural differences (e.g., Brungart, 1999; Wightman & Kistler, 1992), suggesting that there is a particularly tight relationship between the presence of sound stimuli within the horizontal plane (coded by interaural differences) and the allocation of multimodal visual-auditory attention. If crossmodal plasticity coopts mechanisms already at play in the brain of hearing individuals, such as those related with the importance of interaural cues in the allocation of visual attention, then it can be expected that the behavioral advantage demonstrated by deaf individuals for visual stimuli presented in the periphery under some visual tasks will be more prominent for visual stimuli presented within the horizontal plane than for visual stimuli presented in the vertical plane. Interestingly, there are neural data that may be in line with this hypothesis and be suggestive of there being further splits in how different parts of the visual field are processed under congenital deafness. In a recent study, Almeida and colleagues showed that the auditory cortex of congenitally deaf humans represents visual information (Almeida et al., 2015). Specifically, the location of a stimulus in the visual field could be decoded from information processed within the auditory cortex of deaf but not hearing individuals. Importantly, not all aspects of the visual field were equally represented. There was a clear bias towards the representation of locations within the horizontal plane, when compared to those locations within the vertical plane, and towards the representation of locations in the visual periphery, when compared to those in the fovea (Almeida et al., 2015). That is, the auditory cortex of congenitally deaf humans represents visual information, but this information seems to be restricted to what is presented in the periphery and the horizontal plane (Almeida et al., 2015). Moreover, data from non-human mammals (e.g., Meredith & Lomber, 2011;

Roe, Pallas, Hahm & Sur, 1990) suggests that vertical and horizontal visual planes are not equally represented in the auditory system of non-human deaf individuals. For instance, Meredith & Lomber (2011) showed that the extremes of the vertical plane (i.e., the inferior and superior parts) were not represented in the contralateral visual field in the anterior auditory field of deaf cats. Roe et al. (1990) showed that there is a more precise map for the horizontal plane than for the vertical plane in the auditory cortex of deaf ferrets.

These data strongly suggest that there are differences in the behavioral advantage deaf individuals hold in processing visual stimuli when these stimuli are presented in the visual periphery within the horizontal or the vertical planes. Thus, we predict that the superior performance of deaf individuals in visual tasks should be greater for items presented within the horizontal plane than for items presented within the vertical plane. Indeed, we found that behavioral plasticity in deaf humans is strongest for stimuli that are presented along the horizontal plane.

## **Materials and Methods**

### *Participants.*

Fourteen hearing and fourteen deaf individuals participated in the experiment. The sample size was defined based on the availability of deaf individuals willing to take part in the study. Individuals were recruited at an audiologist's office (author GN). 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 the Faculty of Psychology, University of Lisbon. All but one of the 14 deaf participants were congenitally deaf (the remaining participant acquired deafness very early on due to meningitis). Eight of the 14 deaf individuals had severe hearing loss (from 71 to 90 dB binaurally), and the remaining six had profound hearing loss (above 91 dB binaurally). Half of the deaf participants had some knowledge of Portuguese sign language, but only one of them used it as a native language. All of the deaf individuals used hearing aids. All hearing participants reported no hearing impairment or knowledge of Portuguese sign language. Both groups of participants were matched for age and gender, such that each group included individuals between the ages of 18 and 40 (mean age for

hearing = 29.2 years; mean age for deaf = 28.2 years) and each group included 3 females (see Table 1 for a detailed description of the deaf group).

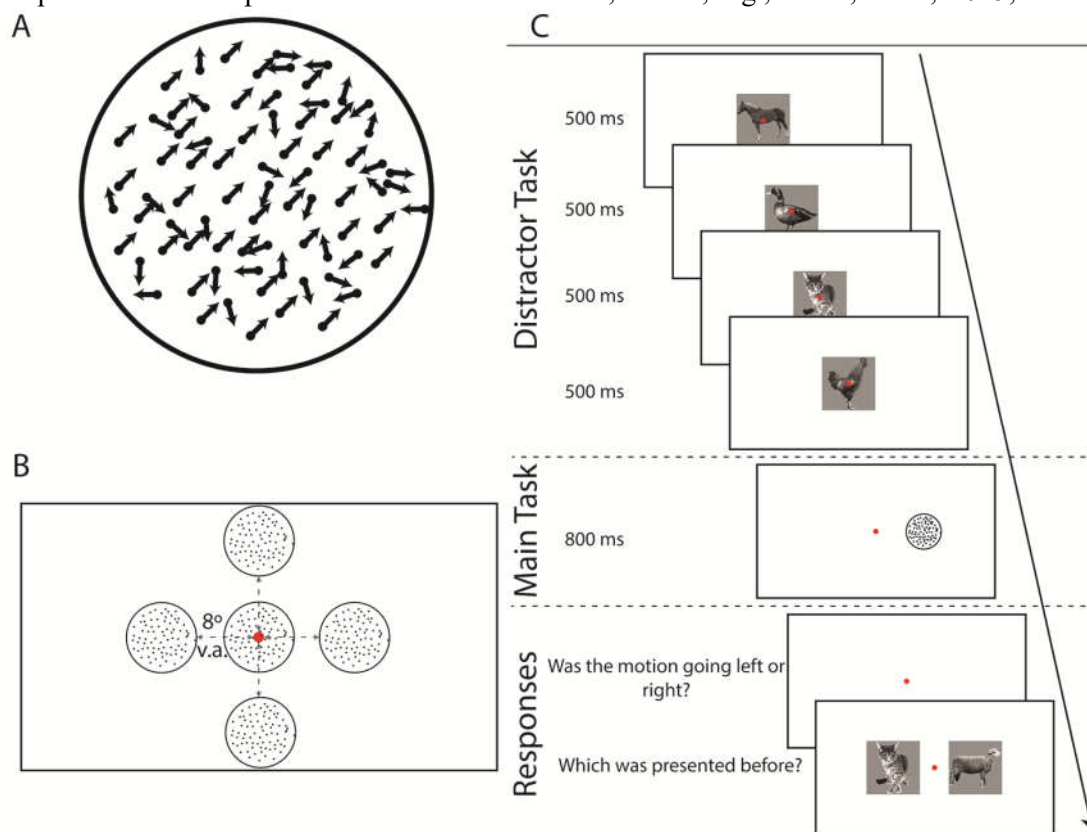
*Stimuli and procedure.*

We used stochastic random-dot patterns to estimate the visual processing capacity of deaf and hearing individuals in different locations of the visual field. These stimuli consisted of a field of 500 white dots presented on a black background within a circular aperture. A proportion of these dots moved in a coherent direction (“left-upward” or “right-upward”), whereas the remaining dots moved in a random fashion. The percentage of dots moving in a coherent fashion was varied randomly across trials between six possible percentages (10%, 15%, 25%, 40%, 60% and 80%) – the higher the percentage the stronger the net motion signal of the stimulus is. The trajectory for each moving dot was very short-lived (about 118 ms), after which the dot disappeared and reappeared in a random location within the circular aperture (see Figure 1A). The motion stimuli could be presented at one of five possible locations: at the center of fixation or in the periphery (with the border of the motion pattern closest to fixation positioned at a distance of about 8 degrees of the visual angle from fixation) within the horizontal plane (left or right of fixation) or the vertical plane (up or down from fixation; see Figure 1B). The motion stimulus stayed on screen for about 800 ms. Participants were instructed to maintain fixation on a red dot presented in the center of the screen for the duration of each trial. Participants were asked to report the perceived direction of motion (“left-upward” vs “right-upward”) by pressing one of two designated keys, and were asked to be as accurate as possible. This task consisted of 576 trials, 192 for each of the three conditions (central presentation, presentation within the horizontal plane, and presentation within

the vertical plane; see Figure 1C for a description of a trial). Participants were tested in a dimly lit room, and the experiment lasted for about 1 hour.

**Figure 1. Examples of the stimuli used and a depiction of the trial structure.** **A)** Here we present an example of the motion stimuli. Arrows represent direction of motion. In this example, 50% of the dots are moving left and upwards (i.e., there is 50% motion coherence); **B)** here we present the five possible locations in which the motion pattern can be presented. Peripheral locations are all equally distant from fixation (8 degrees of the visual angle); and **C)** in each trial, participants were first presented in a concurrent task, immediately followed by the main motion discrimination task. Participants were then asked to report the perceived direction of motion of the motion pattern, and finally were asked to remember which picture was presented in the concurrent task (from two possible pictures).

This primary task was coupled with an attention demanding concurrent task where participants had to monitor a sequence of images – 4 images of faces or animals appeared in rapid sequence (a technique known as Rapid Serial Visual Presentation; RSVP; e.g., Costa, et al., 2015; Kristensen,



Garcea, Mahon, & Almeida, 2016) before the target motion patterns. Each image was presented for 500 ms with no gap between the pictures. After responding to the net direction of motion (i.e., the primary task), participants were presented with 2 images (of the same category as the pictures in the RSVP),



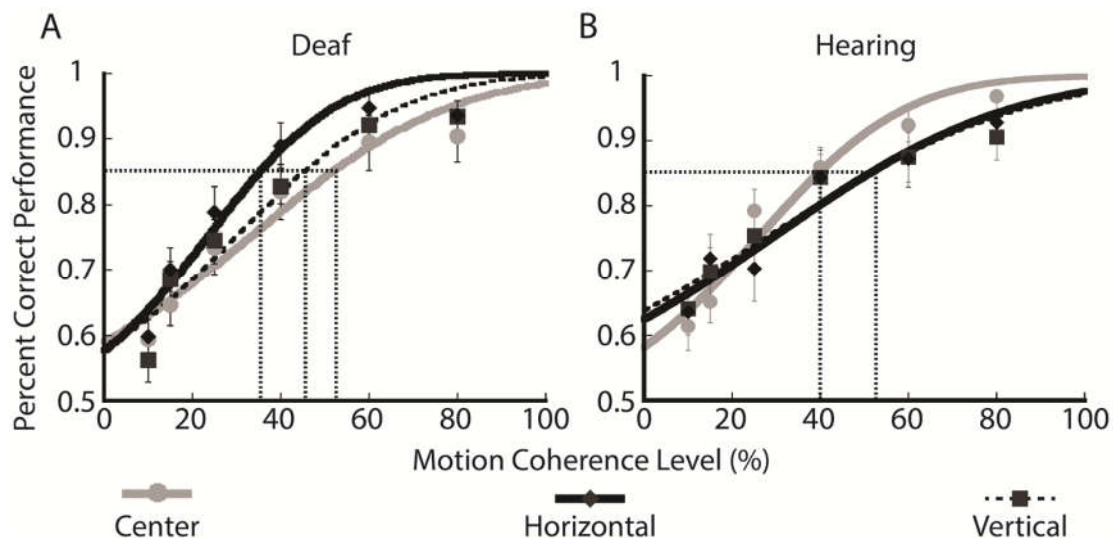
and had to decide which one was presented in the RSVP sequence. The use of a concurrent task, or some sort of attentional taxing procedure, has been routinely used when eliciting enhanced performance on visual tasks in the deaf (e.g., Bavelier et al., 2000; Bosworth and Dobkins, 2002b; for a review see Bavelier et al., 2006), as it may prevent ceiling effects that would mask existing effects.

### *Analysis.*

We measured percent correct performance for each coherence level and condition. These data were fitted with a Probit function, by participant and location (center, horizontal and vertical) independently, using a curve fitting software. From these psychometric functions we calculated the coherence level required for each participant and location to achieve 85% correct performance in determining the direction of motion (i.e., performance that is clearly above chance level but not at ceiling). Planned analysis (Rosenthal, Rosnow, & Rubin, 2000) were computed to compare the performance between locations within each group. Specifically we tested whether horizontal locations led to lower motion thresholds in the deaf but not the hearing group by testing a polynomial quadratic interaction by group and condition (conditions ordered as center, horizontal and vertical: a quadratic contrast under this order would test whether motion thresholds at the horizontal and plane were different from the other two in the predicted way).

## **Results**

All participants presented above chance performance in the secondary task (hearing: average percent correct = 76%, SEM = 2.3%; Deaf: average percent correct = 75%, SEM = 1.9%). We used curve fitting analyses on the data from the primary task. Psychometric fits with  $R^2$  below 0.5 were discarded because we wanted to avoid using psychometric fitted curves that did not achieve a good fit with each participant's data (center locations: data from two deaf and one hearing participants were discarded; horizontal locations: data from one deaf and 3 hearing participants were discarded; vertical locations: data from two hearing participants were discarded). The average  $R^2$  across all participants for each condition were very high (deaf group: 0.77, 0.82, 0.86; hearing group: 0.84, 0.76, 0.79 for the center, horizontal and vertical conditions respectively).



**Figure 2. Compensatory behavior in a direction-of-motion discrimination task.** Average percent correct performance in a direction-of-motion discrimination task for each group in each experimental condition. Participants are presented with moving dots in 3 possible locations: in the center, in the horizontal plane (left and right), or in the vertical plane (up or down). The number of dots moving in the target direction was manipulated, with different levels of motion coherence being presented to the participants. In every trial a percentage of the dots moved in the target direction (i.e., motion coherence level) whereas the other dots moved in random directions. Probit functions were fit to the data for each location condition. The grey curve corresponds to central presentations; the black curve corresponds to presentations in the horizontal plane; and the black-dotted curve corresponds to presentations in the vertical plane. Error bars correspond to SEM values for each coherence level tested. Vertical and horizontal dotted lines correspond to the motion coherence levels required to achieve 85% correct performance (**A**) Deaf individuals require less motion coherence to achieve higher percent correct performance when the motion stimuli are presented in the horizontal plane, when compared to central and vertical positions. Performance for stimuli presented within the vertical plane is not significantly different from that obtained for central presentations; (**B**) Hearing individuals do not show the advantage for the horizontal plane presented by deaf individuals.

Figure 2A and 2B show the psychophysical curves fitted to the average data (N=14 per group) for our deaf and hearing groups respectively. As can be seen in Figure 2A, deaf participants required less motion coherence to achieve better performance when the motion patterns were in the periphery (i.e., black-full and black-dotted curves), than when they were in the center (i.e., grey curve). This advantage was, however, dependent on the actual location in the periphery. Deaf participants were better at discriminating the direction of motion when the motion pattern was within the horizontal plane

(i.e., the black-full curve) than when the motion pattern was within the vertical plane (i.e., black-dotted curve).

These observations were confirmed with statistical testing of the differences between the 85% motion coherence thresholds at each location per group. There was a significant interaction between group and location ( $F(1,22) = 4.98$ ;  $p = 0.036$ ;  $\eta^2 = 0.184$ ), such that for the deaf group the motion thresholds for center, horizontal, and vertical planes followed a quadratic function ( $F(1,11) = 9.46$ ;  $p = 0.011$ ;  $\eta^2 = 0.462$ ), whereas for the hearing group they did not ( $F(1,11) < 1$ ). That is for the deaf group, motion thresholds for the horizontal plane were lower than those for the center and vertical plane, whereas this was not true for the hearing group.

### Discussion

Congenital deaf individuals typically show behavioral profiles on certain non-auditory tasks that differ from those of hearing individuals. Specifically, they may present superior performance in certain tasks that require the processing of information from the unaffected senses or show suboptimal performance in other tasks. Here we tested whether these compensatory strategies were present across the full sensory field of an unaffected sense or were restricted to certain parts of the sensory field. Specifically, we tested whether the advantage for stimuli presented in the visual periphery in certain visual tasks were consistently present across peripheral vision. We found that the behavioral advantage for peripheral visual processing that deaf individuals typically show is restricted to the horizontal plane. Deaf individuals required less motion signal to detect the direction of motion of a random-dot pattern when those patterns were presented in locations within the horizontal plane, when compared to locations in the center of or within the vertical plane. This result was not observed in the performance of hearing participants.

Interestingly, previous studies on behavioral plasticity in the deaf did not report this asymmetry between horizontal and vertical planes (e.g., Bosworth and Dobkins, 2002a). However, most of the extant reports were not set to allow for this difference to stand out. For instance, Bosworth and Dobkins (2002a) showed motion patterns in the visual periphery, but their motion patterns were presented within the four quadrants, not at the actual planes. Moreover, we used a very stringent concurrent task, perhaps more stringent than those used in other reports. In fact, the motion signal necessary for achieving 85%

correct performance in our experiment was higher than the maximum motion signal used in Bosworth and Dobkins's experiment (2002a). By heavily taxing the attentional system of our participants and effectively deploying their resources we are clearly avoiding ceiling effects that could mask processing differences between (peripheral) horizontal and vertical locations.

Available neural data in human and non-human congenitally deaf individuals had already suggested that there were processing differences between information presented at the vertical and horizontal visual planes. For instance, Almeida and colleagues showed there to be a bias towards the representation of visual locations within the horizontal plane at the auditory cortex of congenitally deaf humans, whereas Meredith & Lomber (2011), and Roe and Colleagues (1990) showed a more extended and precise representation of the horizontal visual plane in the auditory cortex of congenitally deaf non-human mammals. One possible understanding of how our results and the neural data on the asymmetries of compensatory plasticity fit together, is that the processing characteristics imposed by the neuroplastic changes happening within the auditory cortex of deaf individuals affect the behavioral performance of deaf individuals on tasks that rely on the unaffected senses.

Interestingly, the role of the neuroplastically-changed auditory cortex in the behavioral performance of non-human deaf individuals has been demonstrated before – work on the deaf cat has shown that deactivation of parts of the auditory cortex obliterate the behavioral advantage deaf cats hold over hearing cats on visual tasks (Lomber et al., 2010; Meredith et al., 2011). These data demonstrate that the processing within the auditory cortex of deaf cats is responsible (and necessary) for the behavioral advantage held by deaf cats. These kind of data are, however, absent for congenitally deaf humans. Because our findings are in direct accordance with extant data on the processing characteristics of the neuroplastically changed auditory cortex of congenitally deaf humans (Almeida et al., 2015), they may be suggestive of a similar relationship in humans. That is, the fact that processing characteristics that have been shown to be present in the neuroplastically changed auditory cortex are also present at the behavioral strategies deaf humans possess, is perhaps suggestive of a role of the neuroplastically-changed auditory cortex in the differential performance of deaf individuals, and particularly in the superior performance deaf individuals show in certain visual tasks when compared to hearing individuals.

However, our results, if anything, only indirectly implicate the neuroplastically-changed auditory cortex in the behavioral advantage presented here for deaf individuals, as we do not have neural data on our participants to accompany their behavioral performance, and our motion detection tasks may not be suitable for addressing this issue. Perhaps further studies should be done in humans using neuromodulation approaches (e.g., Almeida, Martins, Bergström, Amaral, Freixo, et al., 2017; Martins, Fregni, Simis, & Almeida, 2017; Nitsche, Boggio, Fregni, & Pascual-Leone, 2009) in order to causally implicate the neuroplastically-changed auditory cortex. Moreover, while the involvement of the neuroplastically-changed auditory cortex should lead to an advantage for stimuli presented within the horizontal plane, the reverse is not necessarily true as areas other than the auditory cortex may be involved. Nevertheless, because the behavioral effects presented here were restricted to deaf individuals, when compared to hearing individuals, the potential neural locus (or loci) of the behavioral effects reported here should, in principle, be regions that process visual stimuli within the horizontal plane in deaf but not hearing individuals. Interestingly, Almeida et al. (2015) showed that deaf-specific decoding of positions within the horizontal plane was possible only with data from regions located either in left parietal cortex, or in or around the auditory cortex. Thus, these data, together with Lomber et al. (2010)'s data on the causal involvement of the auditory cortex on the behavioral advantage congenitally deaf cats present in certain visual tasks, suggest that the most probable neural locus for the behavioral effect presented here is, effectively, the neuroplastically-changed auditory cortex of deaf individuals. Finally, another potential limitation is the wide range of ages in our sample. As can be seen on Table 1, the age of the majority of our deaf individuals is within one standard deviation of the average age. Nevertheless, because we are testing congenitally deaf individuals, chronological age is fully correlated with the temporal extent of sensorial deprivation. As such, this age range may limit the strength of our results as the older individuals may have a much more neuroplastically changed auditory system than the younger individuals.

One question that stands out from our data concerns the advantage in motion perception at the horizontal plane over the vertical plane in the deaf. It is clear that these two planes are processed differently at the neural level under congenital deafness. As described above, data from human (e.g., Almeida et al., 2015) and non-human mammals (Meredith & Lomber, 2011; Roe et al., 1990) show that

the vertical plane is not as fully represented as the horizontal plane. But why would there be differences in behavioral performance (and neural representation) for these planes? One possibility is related with the central role of interaural differences (necessarily coded within the horizontal plane) in orienting of visual attention in hearing individuals (e.g., Brungart, 1999; Wightman & Kistler, 1992). Perhaps under situations of auditory deprivation, crossmodal plasticity takes advantage of these putative visual-auditory interactions and coopts the deafferented cortex in order to perform similar reorienting tasks over different sensory inputs. This is in line with the current understanding of crossmodal plasticity, and the extant reports on the limits of plasticity (see Bavelier et al., 2006). This is so because the performance advantage for deaf individuals seems to be restricted to tasks that depend on computations that typically benefit from the integration of visual (or tactile) and auditory processes, and/or that happen under very strenuous attentional conditions.

Intriguingly, it has been shown that some congenitally blind individuals present improved auditory localization performance that is dependent on (at least) spectral localization cues (Doucet, Guillemot, Lassonde, Gagné, Leclerc, et al., 2005). This seems to be in relative contradiction with our proposal that the behavioral advantage for items presented in the horizontal plane (and the neural effect presented in Almeida et al., 2015) is related to the importance of interaural differences in the orientation of attention. One possible way to integrate these seemingly contradictory proposals is to suggest that plasticity exploits the functional and anatomical processing characteristics of the deprived (and modified) sensory cortex – in the case of the congenitally blind, neuroplasticity may take advantage of the important functional and anatomical divide between cortical regions dedicated to the upper or lower visual fields (e.g., Danckert & Goodale, 2001; Previc, 1990), and their relationship with visual attention and localization (Ellison & Walsh, 2000; Feng & Spence, 2014; Previc, 1990); whereas under congenital deafness, plasticity may exploit primarily interaural cues, and effectively focusing on the horizontal plane, because of the putative centrality of these cues in sound localization (e.g., Brungart, 1999; Wightman & Kistler, 1992).

Finally, our data may be extremely useful for supporting cognitive interventions on deaf adults that receive a cochlear implant late in life. The success of cochlear implantation decreases abruptly for those interventions performed in adulthood (e.g., Fallon et al., 2008; Kral, 2013; Kral & Eggermont,

2007; Kral & Sharma, 2012; Sharma et al, 2009). Certainly, the extent of neuroplastic changes imposed over the auditory cortex is a major variable in whether implantation is successful. One intriguing possibility that comes out of our data is that this behavioral bias towards the horizontal plane could be used in a visual-auditory bimodal cognitive stimulation program to train the auditory cortex to represent different tones and types of auditory stimuli. Striem-Amit, Almeida, Belledone, Chen, Fang, et al. (2016), testing the same participants as Almeida et al., (2015; Amaral et al., 2016), have recently shown that the typical tonotopic connectivity patterns are still present in congenitally deaf (presumably in parallel with the visual representation of the horizontal plane). Further testing may reveal that there are specific correlations between tonotopic connectivity patterns and the representation of different aspects of the horizontal plane that can be exploited.

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### Author Note

These results were, in part, presented as a poster at the Fourth International Conference on Cognitive Hearing Science for Communication (2017; Linköping, Sweden).

### Context of the Research:

My laboratory (the [http://gaius.fpce.uc.pt/pessoais/jorgealmeida/proaction\\_home.html](http://gaius.fpce.uc.pt/pessoais/jorgealmeida/proaction_home.html)) has been interested, among other things, in how congenital deafness shapes neural processing, and how this affects the behavioral profiles deaf individuals present in certain visual (or non-auditory) tasks. We showed previously that there were particular characteristics of the neuroplastically-changed auditory cortex of congenitally deaf individuals (i.e., the bias towards the horizontal plane) that could be exploited to get at the question of how the differential performance of deaf individuals comes about. This paper is essentially the execution of this idea, and will serve as a catalyst for more experiments trying to determine the causal relationship between neuroplastic changes and behavioral plasticity, as this relationship is central for our understanding of deafness, and of long-term neuroplasticity.



### References

- Almeida, J., He, D., Chen, Q., Mahon, B. Z., Zhang, F., Gonçalves, Ó. F., Fang, F., & Bi, Y. (2015). Decoding visual location from neural patterns in the auditory cortex of the congenitally deaf. *Psychological Science*, 26, 1771-1782.
- Almeida, J., Martins, A.R., Bergström, F., Amaral, L., Freixo, A., Ganho-Ávila, A., Kristensen, S., Lee, D., Nogueira, J., & Rufford, M. (2017). Polarity-specific transcranial Direct Current Stimulation effects on object-selective neural responses in the Inferior Parietal Lobe. *Cortex*, 94, 176-181.
- Amaral, L., & Almeida, J. (2015). Neuroplasticity in congenitally deaf humans. *Revista Portuguesa de Psicologia*, 44, 39-45.
- Amaral, L., Ganho-Ávila, A., Osório, A., Soares, M. J., He, D., Chen, Q., Mahon, B. Z., Gonçalves, O. F., Sampaio, A., Fang, F., Bi, Y. and Almeida, J. (2016), Hemispheric asymmetries in subcortical visual and auditory relay structures in congenital deafness. *European Journal of Neuroscience*, 44, 2334-2339.
- Arnold, P. & Murray, C. (1998). Memory for faces and objects by deaf and hearing signers and hearing nonsigners. *Journal of Psycholinguistic Research* 27, 481-497.
- Barker, D.H., Quittner, A.L., Fink, N.E., Eisenberg, L.S., Tobey, E.A., et al., (2009). Predicting behavior problems in deaf and hearing children: the influences of language, attention, and parent-child communication. *Developmental Psychopathology*, 21(2), 373-392.
- Bavelier, D., & Hirshorn, E. A. (2010). I see where you're hearing: how cross-modal plasticity may exploit homologous brain structures. *Nature neuroscience*, 13(11), 1309-1311.
- Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: where and how?. *Nature Reviews Neuroscience*, 3(6), 443-452.
- Bavelier, D., Dye, M.W.G., & Hauser, P.C. (2006). Do deaf individuals see better? *Trends in Cognitive Sciences*, 10 (11), 512-518.
- Bavelier, D., Tomann, A., Hutton, C., Mitchell, T., Corina, D., Liu, G., & Neville, H. (2000). Visual attention to the periphery is enhanced in congenitally deaf individuals. *Journal of Neuroscience*, 20 (17), 1-6.
- Bosworth, R. G. & Dobkins, K. R. (2002a). Visual field asymmetries for motion processing in deaf and hearing signers. *Brain and Cognition*. 49(1), 170-181.
- Bosworth, R.G., & Dobkins, K.R. (2002b). The effects of spatial attention on motion processing in deaf signers, hearing signers, and hearing nonsigners. *Brain and Cognition*, 49(1), 152-169.
- Boutla, M., Supalla, T., Newport, E.L., & Bavelier, D. (2004). Short-term memory span: insights from sign language. *Nature Neuroscience*, 7(9), 997-1002.
- Brungart, D.S. (1999). Auditory localization of nearby sources. III. Stimulus effects. *The Journal of the Acoustical Society of America* 106(6), 3589-3602.
- Campbell, J. & Sharma, A. (2016). Visual cross-modal re-organization in children with cochlear implants. *Plos One*, 11(1), e0147793.
- Chen, Q., Zhang, M., & Zhou, X. (2006). Effects of spatial distribution of attention during inhibition of return (IOR) on flanker interference in hearing and congenitally deaf people. *Brain Research*, 1109(1), 117-127.

- Conway, C.M., Karpicke, J., Anaya, E.M., Henning, S.C., Kronenberger, W.G. et al., (2011). Nonverbal cognition in deaf children following cochlear implantation: motor sequencing disturbances mediate language delays. *Developmental Neuropsychology*, 36(2), 237–254.
- Costa, S., Gonçalves, O. F., DeLuca, J., Chiaravalloti, N., Chakravarthi, R., & Almeida, J. (2015). The temporal dynamics of visual processing in multiple sclerosis. *Applied Neuropsychology: Adult*, 1-8.
- Danckert, J. & Goodale, M.A. (2001). Superior performance for visually guided pointing in the lower visual field. *Experimental Brain Research*, 137, 303–308.
- Doucet, M.E., Guillemot, J.P., Lassonde, M., Gagné, J.P., Leclerc, C., et al., (2005). Blind subjects process auditory spectral cues more efficiently than sighted individuals. *Experimental Brain Research*, 160(2), 194-102.
- Ellison, A. & Walsh, V. (2000). Visual field asymmetries in attention and learning. *Spatial Vision*, 14(1):3-9.
- Fallon, J.B., Irvine, D.R., & Shepherd, R.K. (2008). Cochlear implants and brain plasticity. *Hear Research*, 238(1-2), 110-117.
- Feng, J. & Spence, I. (2014). Upper visual field advantage in localizing a target among distractors. *Iperception*, 5(2): 97–100.
- Fengler, I., Nava, E., Villwock, A.K., Büchner, A., Lenarz, T., et al., (2017). Multisensory emotion perception in congenitally, early, and late deaf CI users. *PLoS One*, 12(10):e0185821.
- Finney, E.M., & Dobkins, K.R. (2001). Visual contrast sensitivity in deaf versus hearing populations: exploring the perceptual consequences of auditory deprivation and experience with a visual language. *Brain Research: Cognitive Brain Research*, 11, 171–183.
- Finney, E. M., Fine, I. & Dobkins, K. R. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*. 4, 1171–1173.
- Gheysen, F., Loots, G., & Van Waelvelde, H. (2008). Motor development of deaf children with and without cochlear implants. *The Journal of Deaf Studies and Deaf Education*, 13(2), 215–224.
- Hickok, G., Poeppel, D., Clark, K., Buxton, R. B., Rowley, H. A., & Roberts, T. P. (1997). Sensory mapping in a congenitally deaf subject: MEG and fMRI studies of cross-modal non-plasticity. *Human brain mapping*, 5(6), 437-444.
- Horn, D.L., Davis, R.A., Pisoni, D.B., & Miyamoto, R.T. (2005). Development of visual attention skills in prelingually deaf children who use cochlear implants. *Ear and Hearing*, 26(4), 389-408.
- Horn, D.L., Pisoni, D.B., & Miyamoto, R.T. (2006). Divergence of Fine and Gross Motor Skills in Prelingually Deaf Children: Implications for Cochlear Implantation. *Laryngoscope*, 116(8), 1500–1506.
- Hunt, D. L., Yamoah, E. N., & Krubitzer, L. (2006). Multisensory plasticity in congenitally deaf mice: how are cortical areas functionally specified?. *Neuroscience*, 139(4), 1507-1524.

- Karns, C.M., Dow, M.W., & Neville, H.J. (2012). Altered cross-modal processing in the primary auditory cortex of congenitally deaf adults: a visual-somatosensory fMRI study with a double-flash illusion. *Journal of Neuroscience*, 32(28), 9626-38.
- Kral, A. (2013). Auditory critical periods: a review from system's perspective. *Neuroscience*, 247, 117-133.
- Kral, A. & Sharma, A. (2012). Developmental neuroplasticity after cochlear implantation. *Trends Neuroscience*, 35(2), 111-122.
- Kral, A., & Eggermont, J.J. (2007). What's to lose and what's to learn: Development under auditory deprivation, cochlear implants and limits of cortical plasticity. *Brain Research Reviews*, 56(1), 259-269.
- Kral, A., Hartmann, R., Tillein, J., Heid, S., & Klinke, R. (2002). Hearing after congenital deafness: central auditory plasticity and sensory deprivation. *Cerebral Cortex*, 12(8), 797-807.
- Kral, A., Schröder, J.H., Klinke, R., & Engel, A.K. (2003). Absence of cross-modal reorganization in the primary auditory cortex of congenitally deaf cats. *Experimental Brain Research*, 153, 605-613.
- Kristensen, S., Garcea, F.E., Mahon, B.Z., & Almeida, J. (in press). Temporal frequency tuning reveals interactions between the dorsal and ventral visual streams. *Journal of Cognitive Neuroscience*.
- Levanen, S. & Hamdorf, D. (2001). Feeling vibrations: enhanced tactile sensitivity in congenitally deaf humans. *Neurosci. Lett.* 301, 75-77.
- Levanen, S., Jousmaki, V., & Hari, R. (1998). Vibration-induced auditory-cortex activation in a congenitally deaf adult. *Current Biology*, 8, 869-872.
- Loke, W.H., & Song, S. (1991). Central and peripheral visual processing in hearing and nonhearing individuals. *Bulletin of the Psychonomic Society*, 29(5), 437-440.
- Lomber, S.G., Meredith, M.A., & Kral, A. (2010). Crossmodal plasticity in specific auditory cortices underlies visual compensations in the deaf. *Nature Neuroscience*, 13, 1421 - 1427.
- Lyness, R. C., Alvarez, I., Sereno, M. I., & MacSweeney, M. (2014). Microstructural differences in the thalamus and thalamic radiations in the congenitally deaf. *Neuroimage*, 100, 347-357.
- Martins, A. R., Fregni, F., Simis, M., & Almeida, J. (2017). Neuromodulation as a cognitive enhancement strategy in healthy older adults: promises and pitfalls. *Neuropsychology, development, and cognition. Section B, Aging, neuropsychology and cognition*, 24(2), 158-185.
- McCullough, S., & Emmorey, K. (1997). Face processing by deaf ASL signers: Evidence for expertise in distinguishing local features. *Journal of Deaf Studies and Deaf Education*, 212-222.
- Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: the opportunity of change. *Nature Neuroscience*, 11, 44-52.
- Meredith, M. A., & Lomber, S. G. (2011). Somatosensory and visual crossmodal plasticity in the anterior auditory field of early-deaf cats. *Hearing research*, 280(1), 38-47.
- Meredith, M. A., Kryklywy, J., McMillan, A. J., Malhotra, S., Lum-Tai, R., & Lomber, S. G. (2011). Crossmodal reorganization in the early deaf switches sensory, but not behavioral roles of auditory cortex. *Proceedings of the National Academy of Sciences*, 108(21), 8856-8861.

- Neville, H. J. & Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Research*, 405, 268–283.
- Nishimura, H., Hashikawa, K., Doi, K., Iwaki, T., Watanabe, Y., Kusuoka, H., ... & Kubo, T. (1999). Sign language ‘heard’ in the auditory cortex. *Nature*, 397(6715), 116-116.
- Nitsche, M. A., Boggio, P. S., Fregni, F., & Pascual-Leone, A. (2009). Treatment of depression with transcranial direct current stimulation (tDCS): a review. *Experimental Neurology*, 219(1), 14-19.
- Parasnis, I., Samar, V., Bettger, J., & Sathe, K. (1996). Does deafness lead to enhancement of visual spatial cognition in children? Negative evidence from deaf nonsigners. *Journal of Deaf Studies and Deaf Education*, 1(2), 145-52.
- Previc, F.H. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, 13, 519-575.
- Proksch, J., & Bavelier, D. (2002). Changes in the spatial distribution of visual attention after early deafness. *Journal of Cognitive Neuroscience*, 14(5), 687-701.
- Rebillard, G., Carlier, E., Rebillard, M., & Pujol, R. (1977). Enhancement of visual responses on the primary auditory cortex of the cat after an early destruction of cochlear receptors. *Brain research*, 129(1), 162-164.
- Rebillard, G., Rebillard, M., & Pujol, R. (1980). Factors affecting the recording of visual-evoked potentials from the deaf cat primary auditory cortex (AI). *Brain research*, 188(1), 252-254.
- Reynolds, H. N. (1993). Effects of foveal stimulation on peripheral visual processing and laterality in deaf and hearing subjects. *American Journal of Psychology*, 106(4), 523–540.
- Roe, A.W., Pallas, S.L., Hahm, J.O. & Sur, M. (1990). A map of visual space induced in primary auditory cortex. *Science*, 250, 818-820.
- Rosenthal, R., Rosnow, R. L., & Rubin, D. B. (2000). *Contrasts and effect sizes in behavioral research: A correlational approach*. Cambridge University Press.
- Rothpletz, A.M., Ashmead, D.H., & Thorpe, A.M. (2003). Responses to targets in the visual periphery in deaf and normal-hearing adults. *Journal of Speech, Language, and Hearing Research*, 46(6), 1378-1386.
- Sharma, A., Nash, A.A., & Dorman, M. (2009). Cortical development, plasticity and re-organization in children with cochlear implants. *Journal of Communication Disorders*, 42(4), 272–279.
- Stevens, C., & Neville, H. (2006). Neuroplasticity as a double-edged sword: deaf enhancements and dyslexic deficits in motion processing. *Journal of Cognitive Neuroscience*, 18(5), 701–714.
- Striem-Amit, E., Almeida, J., Belledone, M., Chen, Q., Fang, Y., Han, Z., Caramazza, A., & Bi, Y. (2016). Topographical functional connectivity patterns exist in the congenitally, prelingually deaf. *Scientific Reports*, 6, Article number: 29375.
- Wallace, G. & Corballis, M.C. (1973). Short-term memory and coding strategies in the deaf. *Journal of Experimental Psychology*, 99(3), 334-48.
- Wightman, F.L. & Kistler, D.J. (1992). The dominant role of low-frequency interaural time differences in sound localization. *The Journal of the Acoustical Society of America*, 91(3), 1648-61.

Yucel, E. & Derim, D. (2008). The effect of implantation age on visual attention skills. *International Journal of Pediatric Otorhinolaryngology*, 72(6), 869-877.

### Figure Legends

**Figure 1. Examples of the stimuli used and a depiction of the trial structure.** **A)** Here we present an example of the motion stimuli. Arrows represent direction of motion. In this example, 50% of the dots are moving left and upwards (i.e., there is 50% motion coherence); **B)** here we present the five possible locations in which the motion pattern can be presented. Peripheral locations are all equally distant from fixation (8 degrees of the visual angle); and **C)** in each trial, participants were first presented in a concurrent task, immediately followed by the main motion discrimination task. Participants were then asked to report the perceived direction of motion of the motion pattern, and finally were asked to remember which picture was presented in the concurrent task (from two possible pictures).

**Figure 2. Compensatory behavior in a direction-of-motion discrimination task.** Average percent correct performance in a direction-of-motion discrimination task for each group in each experimental condition. Participants are presented with moving dots in 3 possible locations: in the center, in the horizontal plane (left and right), or in the vertical plane (up or down). The number of dots moving in the target direction was manipulated, with different levels of motion coherence being presented to the participants. In every trial a percentage of the dots moved in the target direction (i.e., motion coherence level) whereas the other dots moved in random directions. Probit functions were fit to the data for each location condition. The grey curve corresponds to central presentations; the black curve corresponds to presentations in the horizontal plane; and the black-dotted curve corresponds to presentations in the vertical plane. Error bars correspond to SEM values for each coherence level tested. Vertical and horizontal dotted lines correspond to the motion coherence levels required to achieve 85% correct performance **(A)** Deaf individuals require less motion coherence to achieve higher percent correct performance when the motion stimuli are presented in the horizontal plane, when compared to central and vertical positions. Performance for stimuli presented within the vertical plane is not significantly different from that obtained for central presentations; **(B)** Hearing individuals do not show the advantage for the horizontal plane presented by deaf individuals.

Table 1

*Demographic variables for the deaf group*

Age	Gender	Etiology	Onset of deafness	Un-aided PTA (best ear)	Onset of hearing-aid use (years)	Amount of hearing-aid use (years)	Total duration of deafness (years)	Primary communication strategy
34	Male	Unknown	Since birth	93dB	3	31	34	Oral language
27	Male	Perinatal hypoxia	Since birth	114dB	2	25	27	Oral language
40	Female	Congenital rubella	Since birth	98dB	2	38	40	Oral language
33	Male	Menigitis	3 years old	106dB	4	29	30	Oral language
26	Male	Unknown	Since birth	104dB	2	24	26	Oral language
24	Male	Genetic	Since birth	73dB	2	22	24	Oral language
27	Male	Unknown	Since birth	74dB	3	24	27	Oral language
18	Male	Congenital rubella	Since birth	90dB	1	17	18	Oral language
32	Male	Unknown	Since birth	79dB	5	27	32	Oral language
29	Female	Unknown	Since birth	76dB	5	24	29	Oral language
24	Male	Unknown	Since birth	84dB	2	22	24	Manual language
30	Male	Perinatal hypoxia	Since birth	90dB	2	28	30	Oral language
23	Female	Unknown	Since birth	81dB	3	20	23	Oral language
28	Male	Unknown	Since birth	80dB	4	24	28	Oral language