Unraveling the impact of congenital deafness on individual brain organization

Amaral, Lénia[1], Wang, Xiaosha[2,3*], Bi, Yanchao [2,3,4¥], & Striem-Amit, Ella[1¥]*
[1]*Department of Neuroscience, Georgetown University Medical Center, Washington, DC, USA*
[2]*State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, China*
[3]*Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, China*
[4]*Chinese Institute for Brain Research, Beijing, China*
*These authors contributed equally to this work
¥For correspondence: ella.striemamit@georgetown.edu (Striem-Amit, E.) or ybi@bnu.edu.cn (Bi, Y.)

Abstract

Research on brain plasticity, particularly in the context of deafness, consistently emphasizes the reorganization of the auditory cortex. However, a critical question arises: to what extent do all individuals with deafness show the same level of reorganization? To address this question, we examined the individual differences in deafness functional connectivity (FC), specifically from the deprived auditory cortex. Our findings demonstrate a remarkable differentiation between individuals deriving from the absence of shared auditory experiences, resulting in heightened FC variability among deaf individuals, compared to more consistent FC in the hearing group. Notably, this increased variability is particularly pronounced in regions where FC diverges between the deaf and hearing individuals, reflecting the individual differences in how the brain reorganizes in response to sensory deprivation. Additionally, connectivity to language regions also becomes more diverse in deafness across individuals. Importantly, this does not stem from delayed language acquisition, as it is found in deaf native signers, who are exposed to rich natural language since birth. Further, comparing FC diversity between deaf native signers and deaf delayed signers who were deprived of language in early development, we show that language experience also impacts individual differences, although to a more moderate extent. Overall, our research points out the intricate interplay between brain plasticity and individual differences, shedding light on the diverse ways reorganization manifests among individuals. It further joins findings in blindness, showing that individual differences are affected by sensory experience. Finally, these findings highlight the importance of considering individual differences in personalized rehabilitation for hearing loss.

Keywords: fMRI, plasticity, individual differences, deafness, language, development

Introduction

Neural plasticity, a fundamental property of the brain, refers to its ability to adapt and reorganize in response to sensory input and environmental demands. Meaningful plasticity is found in response to extreme environmental scenarios, such as missing the typical input to an entire sensory channel. Extensive research into neural plasticity in congenital deafness has shown that deafness induces large-scale neural reorganization (e.g., Allen et al., 2013; Almeida et al., 2015, 2018; Amaral et al., 2016; Finney et al., 2003; Lomber et al., 2010; Ruttorf et al., 2023; Scott et al., 2014; for a review see Alencar et al., 2019). For instance, the auditory cortex (AC) in deafness becomes highly responsive to visual stimuli, reflecting a compensatory adaptation to sensory deprivation (e.g., Codina et al., 2017; Hauthal et al., 2013; Simon et al., 2020). Importantly, the reorganization of the AC in deaf individuals also plays a role in language processing, responding to sign language, which uses the visual rather than the auditory modality (Nishimura et al., 1999; Trumpp & Kiefer, 2018). Although most findings in congenital deafness that suggest visual processing in the AC are caused by hearing loss, as opposed to using sign language (Cardin et al., 2013, 2016; Fine et al., 2005), sign language itself also affects cross-modal plasticity - for example in the processing of motion (Bavelier et al., 2001; Codina et al., 2017; McCullough et al., 2012). Therefore, both auditory deprivation and compensatory capacities are important factors when seeking to comprehend the plastic alterations in the AC in deafness. Overall, hearing loss promotes cross-modal plasticity in the AC and beyond it but do all individuals with deafness undergo the same *level* or even *type* of reorganization? Or can reorganization affect deaf people differently, shedding light on the nature of plasticity at the individual level? Recent evidence on blindness suggests that the variability between individuals may even be further increased due to sensory deprivation (Sen et al., 2022). In this study, we showed that people who were congenitally blind have significantly more individual differences in brain connectivity from their deprived visual cortex beyond what is found in sighted controls. This was especially true in areas where connectivity is reshaped by blindness (Sen et al., 2022). This suggests that plasticity may be more variable among people than previously thought. Further, it illustrates the role of postnatal experience, in driving individual differences in brain development. Is the expansion of individual differences due to plasticity a general principle of brain development? If so, we can expect to find increased individual differences in deafness as well.

Testing this question in deafness has an additional theoretical advantage. The postnatal experience which contributes to increased individual differences in blindness encompasses both the absence of typical visual experience and the compensatory use of other senses by the blind. Discerning which of these factors is the primary drive for increased individual differences is challenging in blindness. Blindness tends to be compensated by the use of many different sensory and cognitive compensatory strategies; some individuals read Braille while others have not learned Braille or prefer audiobooks, and different tools utilize audition or touch for navigation and computer use. In deafness, although compensation is not monolithic, and can take the form of relying on lipreading, visual peripheral processing, and sign language, all these compensations rely on the visual modality, and sign language is highly predominant. Therefore, testing signing

deaf individuals allows to some degree to parse the effects of sensory deprivation and compensatory modalities as factors driving individual differences. Should we find increased individual differences in congenital deafness as previously shown in blindness, it would signify that deprivation on its own could generate a greater diversity of developmental outcomes.

Last, deafness is frequently accompanied by a secondary deprivation. Deaf children born to hearing parents who are raised without direct contact to other deaf adults often suffer from delayed language acquisition as they cannot perceive spoken or sign language in their environment (Hall, 2017; Mayberry et al., 2002; Mayberry & Eichen, 1991). This early-onset deprivation has unique effects on brain organization as well (Cheng et al., 2023; Lyness et al., 2013; Twomey et al., 2020; X. Wang et al., 2023). If the absence of experience increase individual variability, would language acquisition delay cause additional variation in the link between the auditory and language systems? Individual variability in neural plasticity highlights the complexity of brain reorganization and adaptation to sensory deprivation but may also affect restoration of hearing. In terms of auditory recovery, hearing aids and cochlear implantation are the main options in auditory rehabilitation. In congenital hearing loss, cochlear implants should be applied in younger, rather than older children, as prognosis for effective cochlear implant decreases over time (Karltorp et al., 2020; Kral & Sharma, 2012; Lyness et al., 2013; Purcell et al., 2021; Sharma & Campbell, 2011). However, even then, the success of their application might be dependent on the level of the reorganization of the AC: an early work showed that in children prior to cochlear implantation the level of metabolism in their cortex, including the AC, predicted their speech perception outcomes (D. S. Lee et al., 2001), suggesting a challenge posed by reorganization to intact sensory restoration. In contrast, more recently, it was shown that recruitment of the broad AC (including language areas) for visual speech in deaf adults positively correlates to auditory speech perception following implantation (Anderson et al., 2017). Therefore, understanding the nuances of brain reorganization and specifically how it may vary among deaf individuals, may enable the implementation of more effective and individualized auditory rehabilitative interventions.

Therefore, the goal of the current study is to use brain connectivity to test if individual variability is modulated by sensory deprivation in deafness, and how it may be affected by the use of less variable compensatory modalities and methods (i.e., vision), or by delayed language acquisition. We examine whether the reorganization of the AC in congenital deafness results in connectivity that is particularly variable across individuals. We predict that higher variability will be observed in deafness, despite the common use of the visual modality and sign language as a predominant adaptations, indicating a significant influence of postnatal sensory deprivation on brain organization. Alternatively, if increased individual variability is not observed for the deaf, this would challenge previous findings from the blind (Sen et al., 2022), arguing against the idea that sensory deprivation promotes individual variation in general, and suggesting instead, for instance, that the differential compensatory strategies in blindness are the driving force of increasing individuals differences. Last, testing the role of delayed language acquisition, we predict that deaf individuals with additional delayed language acquisition may show an additional

increase in their individual connectivity differences, signifying that delayed language acquisition, as a form of short-term deprivation, can also affect brain variability across individuals.

Results

Does auditory cortex FC variability differ between congenitally deaf and hearing individuals?

We first investigated whether deafness causes change to the individual differences in the FC from the auditory cortex (AC). To achieve this, FC maps were assessed within each group, the deaf and hearing groups, for their voxel-wise variability across individuals. This was accomplished through the implementation of a whole-brain voxel-level test for homogeneity of variance (Brown Forsythe test, see **Methods**). We found that multiple regions showed significant inter-subject variability differences in FC between the deaf and hearing groups (**Figure 1A**; see also Supplementary Table 1 for the peaks of this effect). These included areas of the left temporal lobe (superior temporal gyrus – STG, including the auditory association cortex), the bilateral inferior frontal cortex (IFG, including Broca's area), the visual dorsal stream (e.g., bilateral parietal lobe), paracentral lobule, medial superior frontal gyrus, and a small part of the visual cortex. The clusters in the STG and IFG fall, to a great extent, within classically identified language regions (see white outline in **Figure 1A**; mapping language areas from Fedorenko et al. (2010).

In order to determine which group has larger individual differences in these regions, we computed the ratio of variability between the two groups (deaf/hearing) in the areas that showed a significant difference in variability (**Figure 1B**). The deaf show variability over twice as large than the hearing in most of the areas that show change to within-group variability - including the STG and the IFG. It showed lower variability in only one cluster in the left early visual cortex. Thus, the findings from this analysis indicate that as in vision, in typically hearing individuals auditory experience appears to exert a general stabilizing influence on FC, whereas auditory deprivation leads to greater overall variability between individuals in the connectivity of the AC. A single exception is that the deaf had more consistent connectivity between their early auditory and visual cortices. This suggests that even when using a main compensatory modality and more consistent adaptations, as compared to blindness, individual differences dramatically increase due to auditory deprivation.

Is the increased variability (mainly) explained by auditory deprivation?

Our sample of deaf individuals was homogenous in having profound auditory deprivation from early life, but included a mix of native signers and adults who were deaf children to hearing parents, who were taught to sign later in life, and in effect experienced delayed language acquisition. Given that our sample of deaf individuals exhibited varying age of language acquisition, it raises the question of whether the observed FC variability is primarily attributable to delayed language acquisition or to auditory deprivation. To investigate this question, we tested if the increased variability would still be found when comparing native deaf signers to hearing

individuals, all of whom had natural language experience (for sign or spoken language, respectively) from birth through their parents. Our results demonstrated a very similar pattern to the one described above, revealing increased variability in temporal, frontal, and parietal regions (**Figure 1C;** see also Supplementary Table 1). The FC variability is higher in the native deaf individuals when compared to the hearing individuals (**Figure 1D**). Similar findings are seen when comparing the deaf delayed-language and hearing groups (**Supplementary Figure 1**). This outcome suggests that deafness-related factors, even without delayed language acquisition, are sufficient to generate more diverse FC from the AC between individuals and that auditory experience, regardless of language exposure, exerts a broad stabilizing effect on FC.

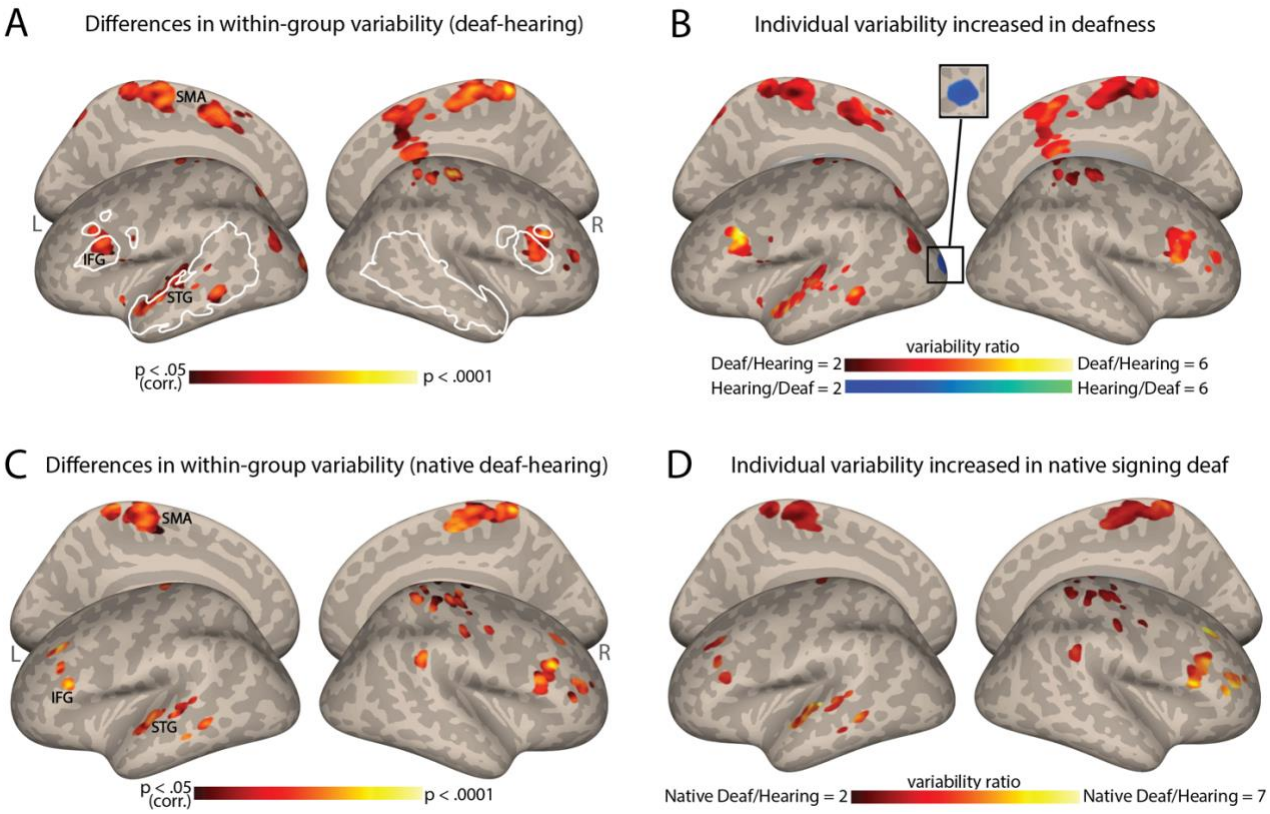

Figure 1. Individual differences in functional connectivity from the auditory cortex increase in deafness. ***A.*** *Significant differences in the inter-individual variability of the AC FC values between deaf and hearing groups (p < .05, corrected for multiple comparisons) are presented on inflated cortical hemispheres. These are found in the left STG (including the auditory association cortex), bilateral IFG (including part of Broca's area), paracentral lobule and the medial superior frontal gyrus, along with the dorsal visual stream.* ***B.*** *The ratio of the within-group variability of AC FC between the deaf and hearing groups is presented (within areas showing variability between the groups. Most areas showing change in variability between the groups display larger individual differences in deafness, including the left auditory cortex and Broca's area.* ***C****. Differences in native signing deaf subgroup and hearing group in their interindividual variability of the auditory cortex FC values (p < .05, corrected for multiple comparisons) replicate the effect of the mixed deaf group (panel A).* ***D****. The ratio of the variability of auditory cortex FC between the native signing deaf and hearing (within areas showing variability difference between the groups). No area showed increased individual differences for the hearing group. Native-signing deaf participants have higher individual differences, despite having no delay in language acquisition.*
Anatomical marks: SMA = Supplementary Motor Area; IFG = Inferior Frontal Gyrus; STG = Superior Temporal Gyrus. The regions outlined in white show some of the language-sensitive regions identified by Fedorenko et al. (2010), including the IFG, the anterior and the posterior temporal parcellations.

Does AC variability increase especially for areas that reorganize in deafness?

To test if this change in individual differences stems from variable outcomes of deafness-related plasticity, we tested if areas which show reorganization in FC are especially susceptible to increased individual differences. We computed the change in FC from the AC between the hearing and deaf groups (**Figure 2A**). Consistent with prior research (e.g., Andin & Holmer, 2022; Ding et al., 2016), deaf individuals showed increased FC to the AC in frontal, temporal, and parietal regions, while for the hearing the connectivity was stronger to sensorimotor areas (**Figure 2B**). We then explored whether regions that had undergone functional reorganization due to deafness also exhibited high variability within the deaf group. We predicted that if plasticity due to deafness results in higher variability, than areas with overall FC change between the groups would also display heightened variability within the deaf group, leading to a correlation between the two spatial maps. We therefore conducted a correlation analysis between the spatial pattern of variability difference observed between the groups (**Figure 1A**) and the spatial pattern of the group effect in terms of AC FC (**Figure 2A**). The Pearson's correlation coefficient between these two maps was highly significant ($r = 0.3$, $p < 0.0001$; confirmed through a permutation test shuffling voxel location across 100,000 iterations; **Figure 2C**). This suggests a link between variability and plasticity: not only is the functional connectivity from the AC more variable in the deaf, but the variability seems especially increased in areas that showed reorganization because of deafness. To test which of the regions that had undergone reorganization had particularly variable plasticity across individuals, we inspected the variability ratio between the deaf and hearing groups in the areas that had group-level changes to FC. We found that all the areas that showed changes to FC exhibited either greater variability within the deaf group (in the STG, parietal and frontal cortex) or similar variability in both groups (**Figure 2D**). No region showed higher variability in the hearing. Together, this suggests that plasticity FC of the AC in deafness is overall linked to more variable outcomes across individuals.

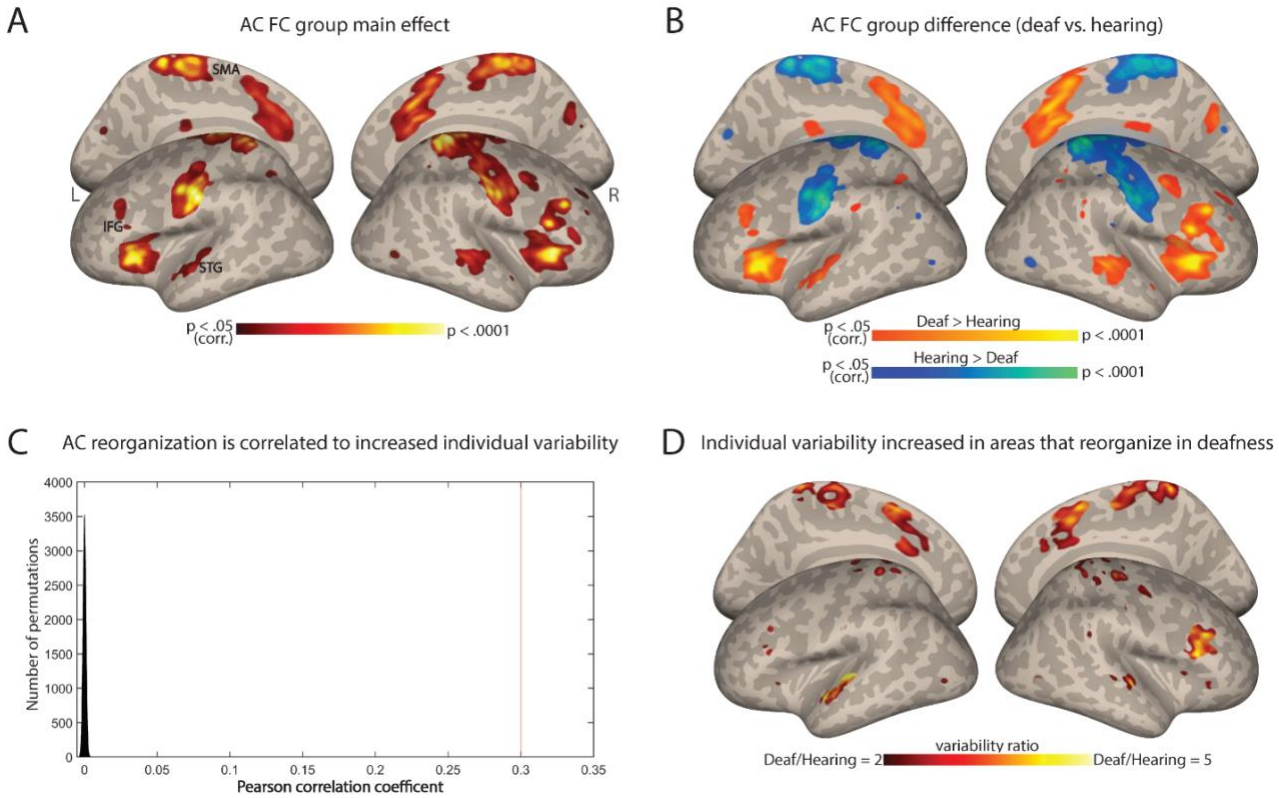

Figure 2. *Individual variability in deafness is related to brain plasticity.* ***A.*** *ANOVA main effect showing which regions are reorganized in deafness (group difference between the deaf and hearing in AC FC; p < .05, corrected for multiple comparisons).* ***B.*** *Direct comparison of AC FC between deaf and hearing groups (p < .05, corrected for multiple comparisons) broadly replicated previous findings, showing broad reorganization in deafness.* ***C.*** *Correlation between regions that show increased individual differences (Figure 1A) with the regions that show reorganization in deafness (panel A) is shown as a red line (r = 0.3) compared with a spatial permutation test (distribution in black); the brain patterns of FC reorganization and of increased individual differences are correlated, suggesting increased individual differences characterizes plasticity in deafness.* ***D.*** *The ratio of the intra-group variability of AC FC between the deaf and hearing groups is shown within areas showing reorganization group-level changes to FC). No area showed increased individual differences for the hearing group. Among the areas showing change in AC FC in deafness, individual differences are overall increased or stable.*
Anatomical marks: SMA = Supplementary Motor Area; IFG = Inferior Frontal Gyrus; STG = Superior Temporal Gyrus.

Does delayed language acquisition affect individual differences?

Finally, we aimed to investigate the independent impact of language exposure and whether delayed language acquisition played an additional role in the heightened variability observed among deaf individuals. To address this, we replicated the FC variability analysis by comparing native deaf signers to delayed deaf signers, equating auditory deprivation. In contrast to the earlier results, which revealed extensive variability change across multiple brain regions, this analysis only identified significant differences between native and delayed deaf signers in four small clusters located in the left hemisphere (**Figure 3A;** see also Supplementary Table 1) in the posterior IFG, posteriorly and superiorly to Broca's area (at the inferior frontal junction), the posterior supramarginal gyrus (pSMG), dorsal visual cortex (precuneus and cuneus), and the orbitofrontal cortex. No differences in variability between the two deaf subgroups was found in the right hemisphere. Interestingly, these regions did not all show a consistent effect in their

direction, but instead increased variability was attributed to both sub-groups for different clusters. FC variability was increased for the delayed deaf individuals both in the inferior frontal junction and the orbitofrontal cortex (**Figure 3B**). In contrast, the native deaf individuals showed higher variability in the pSMG and the dorsal stream (precuneus and cuneus) (**Figure 3B**). Curiously, the areas which showed the difference in variability did not closely correspond to language-related areas. These findings indicate that beyond the broader effects of deafness on individual differences in the FC of the early AC delayed language acquisition can also affect individual differences, albeit to a lesser extent.

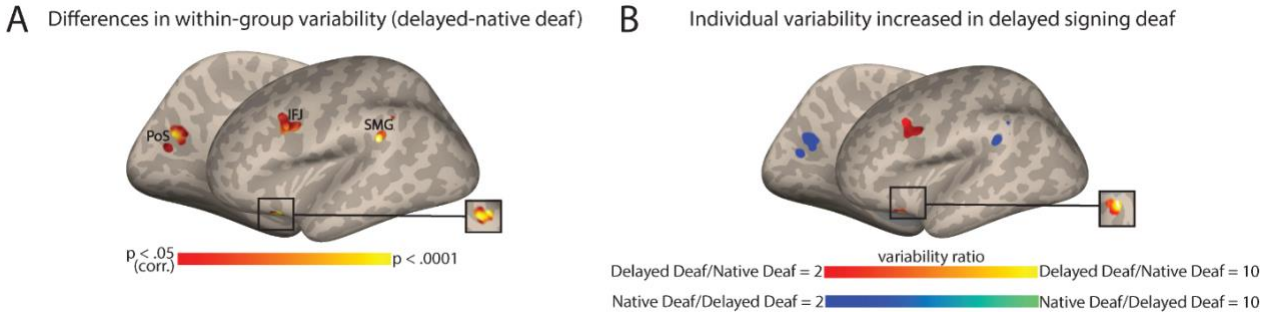

Figure 3. *Auditory cortex FC variability comparison between delayed signing deaf and native signing deaf individuals shows an effect of delayed language acquisition on individual differences.* ***A****. Differences in delayed and native signing deaf subgroups in their interindividual variability of the auditory cortex FC values (p < .05, corrected for multiple comparisons) show changes to individual differences in several left-hemispheric regions (no effects are found in the right hemisphere).* ***B****. The ratio of the variability of auditory cortex FC between the delayed signing and native signing deaf (within areas showing variability between the subgroups in the left hemisphere) shows that individual differences increase due to delayed language acquisition in the inferior frontal junction and orbitofrontal cortex, but that early-onset sign language exposure stabilizes connectivity between the auditory cortex and the supramarginal gyrus and dorsal medial visual cortex (cuneus and precuneus).*
Anatomical marks: PoS = Parietooccipital Sulcus; IFJ = Inferior Frontal Junction; SMG = Supramarginal Gyrus.

Discussion

The findings of this study demonstrate a link between neural plasticity and variability in the auditory cortex (AC) of deaf individuals. Our study has demonstrated that, in comparison to a hearing group, individuals in the deaf group display a greater degree of individual variability in their functional connectivity (FC) from the AC. This is found despite the use of a main adaptation modality to deafness – the use of vision, including for sign language, showing consistency with previous findings of increased individual differences in blindness (Sen et al., 2022), and suggesting the sensory deprivation (blindness and deafness) in itself is a sufficient driver of increased individual differences. Furthermore, there is a relationship between this heightened variability and the adaptive changes occurring within the deprived AC. Specifically, we found that overall, the spatial patterns of plasticity and increased individual differences are correlated, and there is increased variability in many areas functionally connected to the AC that have undergone reorganization due to deafness. Further, some, although more modest, increased variability was found when comparing deaf individuals who had varying degrees of sign language acquisition, suggesting that delayed language acquisition itself also plays an additional significant role in producing different AC functional connections. These findings suggest that although auditory

deprivation in itself may be sufficient to increase individual differences, the variation of the FC patterns in the AC in response to deafness can increase further when considering a combination of auditory experience and delayed language acquisition. Together, these findings show how the interaction of auditory and delayed language acquisition may amplify the spectrum of FC diversity from the AC, allowing for a more comprehensive understanding of the complex factors shaping neural plasticity in response to deafness.

The auditory system, like the visual system, undergoes a critical phase during which its organization is constructed and fine-tuned by sensory experience (Knudsen, 2004). Given the reliance of the AC on auditory input, one would expect a distinct reorganization in cases of auditory deprivation. For instance, while hearing loss induces cross-modal plasticity in the AC, the level of reorganization may vary among individuals with deafness. Recent evidence on blindness (Sen et al., 2022) suggests that the absence of visual experience increases individual differences in brain connectivity. Our research extends this inquiry to a different population experiencing a distinct type of sensory deprivation. Our findings demonstrate how auditory deprivation influences the neural connectivity profile of the deprived AC, introducing variability in the network outcomes. Much of the increased individual differences are found in areas that belong to the language system, including Broca's area (notably bilaterally) and the left STG (**Figure 1A, B**). Therefore, it appears that connectivity between the early AC and many language regions is stabilized or else affected by the use of audition for language in early life and becomes less consistent in its absence. This aligns with prior research demonstrating significant FC alterations between the AC and the language network in deaf infants and children (Shi et al., 2016; S. Wang et al., 2019). Our findings indicate that the FC variability originating from the AC is primarily driven by higher variability within the deaf group. Notably, only a cluster in the left early visual cortex exhibits higher variability in its FC from the auditory cortex in the hearing group. This suggests a potential stabilizing impact of auditory deprivation on the interaction between the auditory and visual cortices, possibly due to the prevalent use of vision for adaptation. Overall, these results coupled with those of Sen et al. (2022) highlight the impact of postnatal sensory experience in promoting consistency in brain organization, suggesting a general principle of brain development of the sensory systems. Further, it extends them by showing that such diversification of brain connectivity may occur even without broadly different compensatory senses and strategies being used, such that deprivation in itself suffices to develop more variable brain networks across individuals.

The results of this study also provide evidence for the role of neural plasticity in generating diverse individual patterns of brain connectivity. Our finding that the exhibited heightened AC FC variability by the deaf group corresponds spatially to regions that reorganize in deafness, suggests that the increased variability may be attributed to the reorganization and adaptation of neural circuits in response to auditory deprivation. Although not all areas that changed their mean FC to the auditory cortex showed increased variability in the deaf group, we found higher AC FC variability in regions such as the STG, inferior frontal cortex, and premotor cortex/supplementary motor area (SMA). These same brain regions exhibited functional reorganization in response to deafness, as illustrated in **Figure 2B**, consistent with prior research

emphasizing functional changes following auditory deprivation (e.g., Andin & Holmer, 2022; Ding et al., 2016). Importantly, changes in connectivity of the AC reflect the change in its function in deafness. Studies have shown that the AC can be activated in deaf individuals when performing parallel visual tasks, indicating a shift in functional activation from auditory to visual processing (e.g., Almeida et al., 2015; Benetti et al., 2017, 2021; Bola et al., 2017; Bottari et al., 2014; Butler et al., 2017; Finney et al., 2001; Lomber et al., 2010; Meredith & Lomber, 2011; Petitto et al., 2016; Scott et al., 2014), albeit typically for the same type of functional computation (Cardin et al., 2020; Heimler et al., 2015; Lomber, 2017; Pascual-Leone & Hamilton, 2001). Some of these areas show a direct link to sign language: for instance, deaf individuals who are proficient in sign language have exhibited a larger SMA in comparison to hearing non-signers, a difference attributed to the finger movements required for fingerspelling (Kumar & Mishra, 2018). Interestingly, in addition to finding increased variability in connectivity for areas that increase their connectivity in deafness, we also found higher AC FC variability in regions that show a decreased FC to the temporal lobe in deafness, specifically the somatosensory cortex (e.g., Andin & Holmer, 2022; Bonna et al., 2021; Ding et al., 2016). Here too, previous research has identified differences in somatosensory involvement between deaf and hearing individuals, which has been linked to sign language and visual processing (Bonna et al., 2021; Okada et al., 2016). Therefore, it appears that any type of plasticity in the connectivity of the AC, regardless of its direction (increased or decreased FC), may manifest variably across individuals.

In addition to the effect of deafness itself, we have also demonstrated how a particular additional factor, namely language experience, may affect variations in FC of the AC. Deaf individuals who have had exposure to sign language from birth, for example, appear to exhibit more consistent connectivity between the AC and the left inferior frontal lobe, as well as the orbitofrontal cortex, compared to those who had experienced delayed language acquisition in early development (**Figure 3B**), suggesting that sign language early experience consolidates this connectivity pattern. In contrast, the connectivity to the supramarginal gyrus and the cuneus/precuneus is more consistent in people who experienced delayed language acquisition in addition to deafness. Although we only speculate why these areas show such interactions, these findings highlight the complex interplay between sensory experience, language acquisition, and neural plasticity in shaping the individual patterns of FC of the AC. However, these outcomes did not align with our initial hypothesis, which anticipated a more pronounced effect of increased individual differences in delayed signers, especially within the language network. This may be since the observed variations in brain connectivity from early AC are primarily attributed to auditory deprivation, rather than delayed language acquisition. In turn, this could be both due to the early AC function as primarily responsive to auditory stimulation as well as to the fairly early maturation of this region (Kral & O'Donoghue, 2010), which may make it more susceptible to auditory deprivation, rather than to delayed language acquisition itself. This conclusion is further reinforced by our analysis targeting a subgroup of the deaf, which included native signers: the findings showed similar patterns of increased individual variability for FC within this subgroup as compared to the hearing (**Figure 1C, D**) compared to a more extensive analysis involving both native and nonnative signers (**Figure 1A, B**). Curiously, we have also tested if increased individual

differences may then be found in the connectivity from Broca's area in the case of delayed language acquisition and did not find any significant effect. Though this may be due to insufficient power, this evidence emphasizes that the increase in individual differences in FC within the AC, and possibly beyond it, during deafness are primarily attributed to auditory deprivation. An additional variable that may contribute to the observed outcomes is the comparable language abilities within our cohort of delayed signers. In fact, all deaf participants self-reported consistent levels of sign language proficiency, a factor that is typically affected following delayed language acquisition (Bogliotti et al., 2020; Caselli et al., 2021; Cheng & Mayberry, 2021; Tomaszewski et al., 2022). Furthermore, a subset of delayed deaf signers acquired sign language before the age of 6 (N = 6, see also Supplementary Table 2), potentially rendering them less susceptible to the impact of language deprivation. To further elucidate these findings, future investigations should include a more diverse sample, specifically in terms of sign language acquisition age, in order to comprehensively address this aspect.

Finally, hearing aids and cochlear implants represent the primary approaches in auditory rehabilitation. The effectiveness of these treatments, especially cochlear implantation, is intricately linked to the extent of reorganization within the AC (Feng et al., 2018; Heimler et al., 2014, 2015; D. S. Lee et al., 2001; H.-J. Lee et al., 2007). The ability to regain a lost sense (i.e., hearing) is likely influenced by the preservation of the auditory system, as cross-modal reorganization for a different function may hinder its capacity to process information from the original modality and computation. Although this link is nuanced, given that some portions of the AC appear to reorganize for parallel functions to those they typically perform (Cardin et al., 2020; Heimler et al., 2015; Lomber, 2017; Pascual-Leone & Hamilton, 2001), the diverse reorganization levels showed in this study hold potential clinical significance for auditory rehabilitation. This is particularly true when considering the larger individual differences in how strongly the AC connects to the language system (**Figure 1B**), where a disconnect may form between the reorganized role in visual language and auditory feed-forward roles. This research offers valuable insights into the diversity of reorganization patterns observed in deaf individuals, highlining the importance of more precise and effective auditory rehabilitation strategies. Additionally, this study highlights the imperative of acknowledging and considering differences between hearing and deaf individuals, particularly when employing normative data in clinical contexts (e.g., neurosurgery). The recognition of variability in brain organization among diverse populations underscores the necessity for tailored approaches in clinical practices, ensuring more accurate and effective interventions for deaf individuals.

It is worth noting that we assessed individual differences based on FC and not activations in response to a task. Although it would be prudent for future research to explore this aspect, we expect that individual patterns of plasticity in the AC connectivity remain relatively consistent across different time periods and states. FC patterns of typically developed individuals have been shown to be primarily shaped by common group and stable individual features, and not by time, state or task (Finn et al., 2015; Gratton et al., 2018; Tavor et al., 2016) . Further, we have recently shown that individual FC patterns are stable across time and state even in the context of plasticity

due to visual deprivation (Amaral et al., 2023). Therefore, there should not to be meaningful differences between resting-state and task FC networks.

In conclusion, this study demonstrates that the lack of auditory experience results in increased individual differences in brain organization. Notably, this increased variability is prominent in language areas and regions undergoing reorganization in response to deafness, highlighting the intricate relationship between brain plasticity and individual differences. Furthermore, our findings indicate that this variability is not solely influenced by sensory deprivation due to deafness; deprivation from language during early life also plays a role in shaping this variability. Ultimately, these outcomes underscore the significance of tailoring rehabilitation strategies to match the unique patterns of plasticity seen in individuals with sensory impairments, including those with deafness.

Methods

Participants

We recruited 39 congenitally or early deaf adults and 33 hearing college students (15 males, mean age 21.97 ± 2.58 years, range: 18–28 years, all native Mandarin Chinese speakers; see **Table 1** for the detailed characteristics of the participants). All of them possessed normal or corrected-to-normal vision, and their majority was right-handed (with the exception of three deaf individuals), as determined by the Edinburgh inventory (Oldfield, 1971). All deaf participants indicated severe or profound deafness from birth, except for one native signer and three delayed signers who reported becoming deaf before the age of 2 due to medication side effects. Hearing thresholds (available in 23 deaf participants) confirmed severe to profound hearing loss, with thresholds ranging from 85 to 120 decibels (dB). Prior to their involvement in the study, all participants provided written informed consent and received monetary compensation for their participation. The research protocol was reviewed and approved by the Human Subject Review Committee at Peking University, adhering to the principles outlined in the Declaration of Helsinki.

The deaf participants were divided into two distinct subgroups. The first subgroup, referred to as "native signers", consisted of 16 individuals (11 males). These individuals were born to deaf parents and were exposed to Chinese Sign Language (CSL) shortly after birth. The second subgroup, known as "delayed signers" (nonnative signers) comprised 23 individuals (12 males). These participants were born into hearing families and began learning CSL after enrolling in special education schools, with the age of CSL initiation ranging from 4 to 10 years.

All participants with hearing impairment completed a background questionnaire, in which they provided information about their hearing loss conditions, history of language acquisition, and educational background. All deaf participants in the study received formal education within special education programs starting from elementary school. The two deaf groups were carefully matched on various demographic variables, including gender, age, and years of education ($p > .15$). Additionally, in terms of language skills, both deaf groups were matched in terms of self-reported proficiency in CSL comprehension, production, and lipreading skills ($p > .34$). At the time of testing, one native signer and four delayed signers were using hearing aids, while others either had never used hearing aids (six native signers and five delayed signers) or had used them for

varying durations (nine native signers and fourteen delayed signers, with usage spanning from 0.5 to 20 years). It is important to note that speech comprehension was reported as very poor, even when hearing aids were employed.

The hearing group and the deaf group were matched based on gender and years of education ($p > .15$), but there was a significant age difference between these two groups ($p < .05$). Given this significant age difference, we used age as a covariate in our FC analyses, and the differences in variability were assessed after statistically accounting for the age variable.

Table 1. Participants' demographic information.

	Native deaf signers (N = 16)	Delayed deaf signers (N = 23)	Hearing non-signers (N = 33)
Age of Sign Language Acquisition	0 ± 0	6.91 ± 1.62	N/A
Age	28.50 ± 7.13	27.09 ± 5.87	21.97 ± 2.54
Years of Education	14.13 ± 2.31	15.09 ± 1.41	15.03 ± 1.93
Gender	11 M, 5 F	12 M, 11 F	15 M, 18 F

Image acquisition

Functional and structural MRI data were collected using a Siemens Prisma 3T Scanner with a 64-channel head-neck coil at the Center for MRI Research, Peking University. Functional data were acquired with a simultaneous multi-slice echoplanar imaging sequence supplied by Siemens (62 axial slices, repetition time [TR] = 2000 ms, echo time [TE] = 30 ms, multi-band factor = 2, flip angle [FA] = 90°, field of view [FOV] = 224 mm × 224 mm, matrix size = 112 × 112, slice thickness = 2 mm, gap = 0.2 mm, and voxel size = 2 mm × 2 mm × 2.2 mm). A high-resolution 3D T1-weighted anatomical scan was acquired using the magnetization-prepared rapid acquisition gradient echo sequence (192 sagittal slices, TR = 2530 ms, TE = 2.98 ms, inversion time = 1100 ms, FA = 7°, FOV = 224 mm × 256 mm, matrix size = 224 × 256, interpolated to 448 × 512, slice thickness = 1 mm, and voxel size = 0.5 mm × 0.5 mm × 1 mm).

Image preprocessing

We used SPM12 (Welcome Trust Centre for Neuroimaging, London, UK), run in Matlab R2018b (Mathworks, Inc., Sherborn, MA, USA), for processing and analysis of structural and functional data. For each participant, the first four volumes of each functional run were discarded for signal equilibrium. The remaining functional data were slice-time corrected to the first slice (middle slice in time) and corrected for head motion to the first volume of the first session using 7th degree b-spline interpolation. All participants had head motion less than 2mm/2°, except for one hearing participant that showed excessive head motion in 2 runs which were excluded from analysis. Structural images were coregistered to the first functional images. Functional data were then normalized to MNI anatomical space using a 12-parameter affine transformation model in DARTEL (Ashburner, 2007) and resampled to 2 mm^3 voxel size prior to applying a 6 mm FWHM Gaussian filter.

Stimuli and procedure

During the fMRI scanning, the participants performed a semantic task whose predictors were regressed out to focus on the underlying FC patterns. Design-regressed task data has been extensively used in the past to calculate FC (e.g., Amaral et al., 2021; Gratton et al., 2018; Norman-Haignere et al., 2012; Walbrin & Almeida, 2021), and it has been shown that it effectively leads to similar FC estimates as when using resting scans (Fair et al., 2007). Stimuli comprised a set of 90 written words. This set consisted of 40 concrete/object words and 50 abstract/nonobject words, the latter lacking explicit external referents. Participants were given instructions to visually examine each of these 90 target words, contemplate their meanings, and engage in an oddball one-back semantic judgment task (Wang et al., 2023).

Each participant completed a total of 10 runs of task fMRI scanning, with each run lasting for 360 seconds. One native signer completed only eight runs and subsequently withdrew from the study due to discomfort, so we analyzed 8 runs for this subject. In each run, there were 90 target word trials, each lasting for 2.5 s, as well as 14 catch trials, also lasting 2.5 s each. For more details about this experiment please see X. Wang et al. (2023).

Functional connectivity analysis

Functional connectivity (FC) was computed using the CONN Toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). Time courses were extracted from the 10 runs after regressing out the task predictors, and potential confounding effects were estimated and removed separately for each voxel and for each participant and run. In addition, functional data were denoised using a standard denoising pipeline (Nieto-Castanon, 2020) including the regression of potential confounding effects characterized by white matter timeseries, CSF timeseries, motion parameters, session and task effects, and simultaneous bandpass frequency filtering of the BOLD timeseries (Hallquist et al., 2013) between 0.01 Hz and 0.1 Hz.

Seed region of interest. The seed region for the early auditory cortex (AC) was defined using the atlas provided by the CONN toolbox (Harvard-Oxford Atlas distributed with FSL, (Jenkinson et al., 2012). We extracted the Heschl's Gyrus parcellation (broadly corresponding to the location of the primary AC) for both hemispheres and used it as our seed region for the FC analysis.

Functional connectivity variability analysis. Seed-based connectivity maps for each subject were estimated characterizing the spatial pattern of FC with the seed area (bilateral Heschl's Gyrus). FC strength was represented by Fisher-transformed bivariate correlation coefficients from a weighted general linear model, modeling the association between their BOLD signal timeseries. To examine whether there were differences in the interindividual variability of FC values between the two groups, namely the deaf and hearing participants, we conducted the Brown–Forsythe test for equal variance (**Figure 1A**). The Brown–Forsythe test (Brown & Forsythe, 1974) is a homogeneity of variance test like Levene's test, conventionally used to test for variability differences, but uses the median instead of the mean, safeguarding against false positives in cases of skewed data distribution (Olejnik & Algina, 1987). The minimum significance level for all presented results was established at $p < .05$, corrected for multiple comparisons within the gray matter volume using the spatial extent method (a set-level statistical inference correction; (Forman et al., 1995; Friston et al., 1994). Correction was based on the Monte Carlo simulation

approach, extended to 3D datasets using the threshold size plug-in for BrainVoyager QX (Brain Innovation, Maastricht, Netherlands). To inspect the direction of the variability group effect, and determine which group had higher variance, we computed the ratio of variability between the groups (Variability Deaf/Variability Hearing, **Figure 1B**; (Sen et al., 2022)) for each voxel showing a significant Brown–Forsythe test effect ($p < .05$, corrected). We also conducted equivalent analyses on a subset of the deaf participants, with our investigation centering on the roots of the differences in individual variability, and whether they stem from auditory deprivation (deafness) or from late exposure to language. To test the role of auditory deprivation, we compared deaf individuals who are native signers to hearing participants (**Figure 1C**), both populations having access to full language (spoken and CSL, respectively) from birth. To test the role of delayed language acquisition, we compared native signing deaf individuals to deaf individuals who acquired sign language at a later stage (**Figure 3**).

Finally, in addition to the variability analysis, FC data was also analyzed to directly compare the connectivity between the groups, with a one-way ANOVA (**Figure 2A**). To inspect the direction of reorganization in AC FC, we computed a *post hoc* t-test comparing FC between the groups (deaf vs. hearing, **Figure 2B**). To quantitatively examine the link between reorganization in deaf individuals and its impact on variability, we conducted a comparative analysis between the spatial pattern of FC variability (**Figure 1A**) and the spatial pattern of reorganization observed in the deaf (**Figure 2A**). This was done with the unthresholded maps to correlate the spatial pattern at large between these statistical effects. This was achieved by calculating the Pearson's correlation coefficient between these maps, specifically within the gray matter (**Figure 2C**). The significance level for the correlation was obtained using a permutation test (100,000 iterations), randomly shuffling voxels for each iteration and convolving each random map with a Gaussian kernel based on data smoothness estimation to account for spatial autocorrelation. The resulting permutation distribution was then compared with the previously obtained Pearson's correlation coefficient. Finally, we also inspected the variability ratio within the areas that showed reorganization in deafness (**Figure 2D**).

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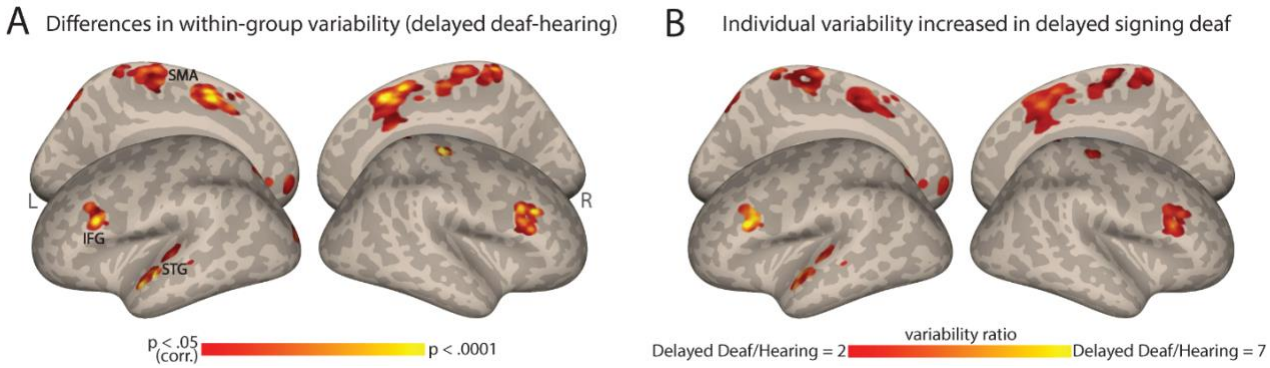

***Supplementary Figure** 1. Auditory cortex FC variability difference between delayed signing deaf and hearing individuals. **A**. Differences in delayed signing deaf subgroup and hearing group in their interindividual variability of the auditory cortex FC values (p < .05, corrected for multiple comparisons). **B**. The ratio of the variability of auditory cortex FC between the delayed signing deaf and hearing (within areas showing variability difference between the groups) replicates the effects seen in when comparing the hearing and mixed deaf group. No significant increase in variability were found for the hearing group.*
Anatomical marks: SMA = Supplementary Motor Area; IFG = Inferior Frontal Gyrus; STG = Superior Temporal Gyrus.

Supplementary Table 1. MNI coordinates for the FC variability analyses.

		Deaf vs. Hearing (peak F-value) Fig. 1A	Deaf Native vs. Hearing (peak F-value) Fig. 1C	Deaf Delayed vs. Hearing (peak F-value) Supp. Fig. 1	Deaf Delayed vs. Deaf Native (peak F-value) Fig. 3A
Left Hemisphere	Superior Temporal Gyrus	-56 -4 -4 (23.1)	-56 -16 6 (17.4)	-58 10 -8 (22.8)	
	Middle Temporal Gyrus	-64-44 0 (17.3)	-64 -28 -2 (16.9)		
	Inferior Frontal Gyrus	-42 20 24 (15.9)	-48 28 20 (28.5)	-44 18 24 (18.2)	
	Middle Frontal Gyrus		-36 30 36 (25.7)		
	Inferior Frontal Junction				-32 4 28 (13)
	Visual V3A	-20 -96 16 (17.7)		-14 -94 20 (18)	
	Angular gyrus	-64 -44 0 (17.3)			
	Lateral Occipital Cortex (dorsal stream)	-16 -66 50 (18.3)			
	Supramarginal Gyrus				-50 -42 34 (24.1)
	Precuneus				-18 -64 26 (12.1)
	Orbitofrontal cortex				-26 16 -24 (16.3)
	Superior Parietal Lobe	-16 -66 50 (18.3)			

	Inferior Parietal Lobe	-38 -84 32 (12.1)		
	Precentral Gyrus	-6 -24 54 (17.7)		
	Pre Supplementary Motor Area	-6 8 54 (15.8)		
Right Hemisphere	Postcentral Gyrus	12 -42 70 (23.2)	-12-42 72 (17.9)	14 -44 70 (15.5)
	Precentral Gyrus	28 -26 54 (22.1)		28 -26 54 (18.6)
	Pre Supplementary Motor Area	0 8 50 (20.1)		0 10 50 (21.9)
	Supplementary Motor Area		4 -16 54 (24.3)	6 -14 54 (16.4)
	Cingulate Cortex	4 8 28 (14.6)		
	Inferior Frontal Gyrus	44 22 24 (23.8)	48 22 24 (28.2)	44 22 24 (22.1)
	Middle Frontal Gyrus		56 24 30 (10.2)	
	Frontal pole	48 48 10 (15.1)	46 48 12 (18.8)	
	Supramarginal gyrus		66 -38 40 (17.1)	

Supplementary Table 2. Age of sign language acquisition for the delayed signing deaf group.

Subjects	**Age of sign language acquisition**
Sub 1	7
Sub 2	5
Sub 3	8
Sub 4	8
Sub 5	8
Sub 6	10
Sub 7	9
Sub 8	7
Sub 9	4
Sub 10	6
Sub 11	7
Sub 12	6
Sub 13	5
Sub 14	8
Sub 15	7
Sub 16	5
Sub 17	5

Sub 18	5
Sub 19	9
Sub 20	6
Sub 21	8
Sub 22	7
Sub 23	9