Neuroscience

Unraveling the impact of congenital deafness on individual brain organization

Reviewed Preprint
v2 •

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Léniaa, Xi Amaaasn, Yuan cWa, Eol Bi Stiem-Amit

eLife Assessment

Abstract

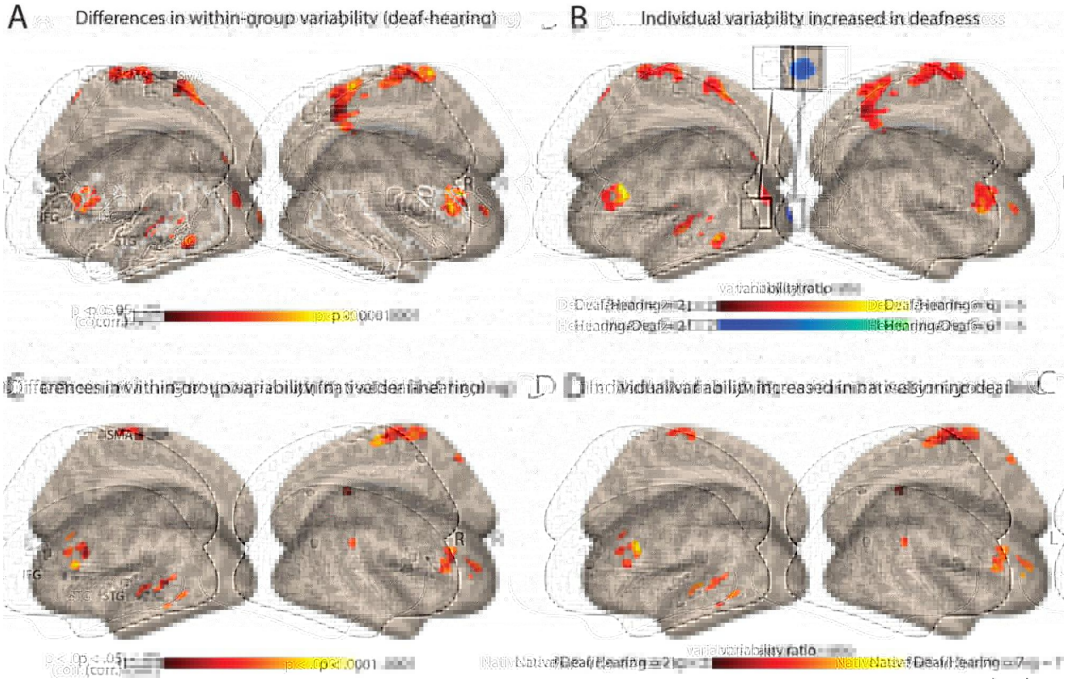
Short Report Neuroscience

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 neural reorganization (e.g., [redacted]; for a review see [redacted]). For instance, the auditory cortex (AC) in deafness becomes highly responsive to visual stimuli, reflecting a compensatory adaptation to sensory loss (e.g., [redacted]). 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 ([redacted]). Although most findings in congenital deafness that suggest visual processing in the AC are caused by hearing loss, as opposed to using sign language ([redacted]), sign language itself also affects cross-modal plasticity - for example in the processing of motion ([redacted]). Therefore, both hearing loss 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 loss ([redacted]). 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 ([redacted]). 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 opens an additional question. 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 ([redacted]). This early-onset deprivation has unique effects on brain organization as well ([redacted]). Therefore, testing individual differences in deafness allows testing a secondary question: If the absence of experience increases individual variability, would language acquisition delay cause additional variation in the link between the auditory and language systems? Or does only early-onset and long-lasting input loss cause such diversification? Last, individual variability in neural plasticity may also impact the 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 the efficacy of cochlear implants decreases if implemented later ([redacted]). 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



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exception is that the deaf had more consistent connectivity between their early auditory and visual cortices. This suggests that as in vision loss (S), individual differences dramatically increase due to deafness.

Is t e s d c v r x i p l b y i l n e d g r b(m g

Our sample of deaf individuals was rather homogenous in having severe to profound hearing loss from early life. However, it 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 ages of language acquisition, it raises the question of whether the observed FC variability above is primarily attributable to delayed language acquisition or to hearing loss. 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 medial regions (**Figure 1C**; see also **Table S1**). The FC variability is higher in the native-signing deaf individuals when compared to the hearing individuals (**Figure 1D**). Similar findings are seen when comparing the deaf delayed-language and hearing groups (e.g., for the IFG, **Figure S2**). 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.

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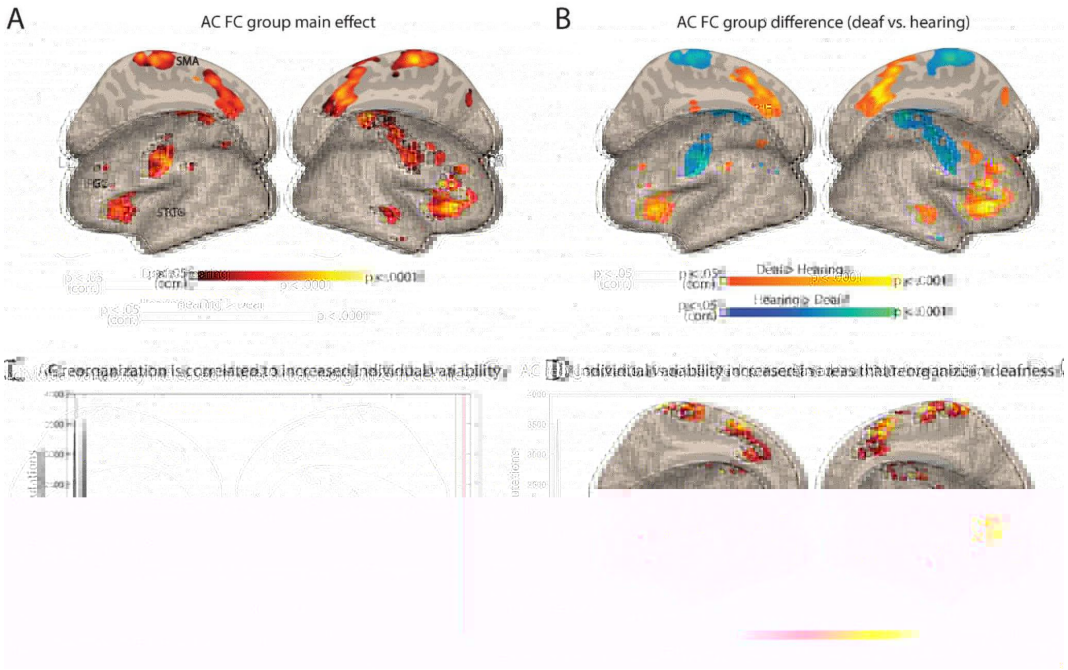
To test if this change in individual differences stems from variable outcomes of deafness-related



Fi ge u r2 .

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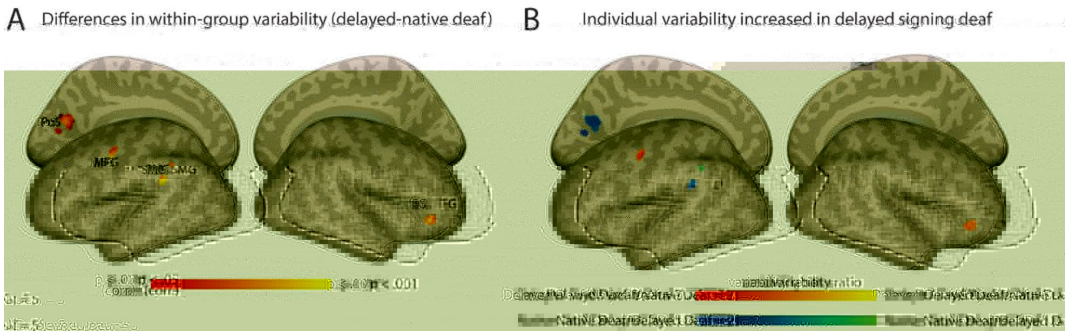
Does delayed language exposure contribute to the variability?

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 deaf native signers to deaf delayed signers, equating hearing loss. In contrast to the results above, 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 (**Figure 3A**; see also **Table S1**) in the left posterior Middle Frontal Gyrus (pMFG), close to the Precentral Gyrus (PreCG), the left posterior supramarginal gyrus (pSMG), left dorsal visual cortex (precuneus and cuneus), and the right anterior inferior frontal gyrus (aIFG). 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 deaf delayed signing individuals both in the left MFG and the right aIFG (**Figure 3B**). In contrast, the deaf native signing individuals showed higher variability in the pSMG and the dorsal stream (precuneus and cuneus) (**Figure 3B**). Interestingly, the two areas that had increased variability in delayed signers closely corresponded to language-related areas (e.g., pMFG and aIFG). 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.

Could other principal individual factors contribute to deafness?

Our results so far suggest that the early lack of hearing experience (i.e., congenital deafness) is the primary factor driving AC-FC variability. However, even congenital deafness is not completely homogenous, and other factors related to partial hearing experience could also contribute to this individual variability among the deaf. For instance, the degree of hearing loss and the use of hearing aids, which provide residual hearing (even if not sufficient for language comprehension in the case of our participants), might also influence individual differences. To test this, we computed the correlation between AC-FC and three factors related to hearing experience: the age when hearing aids were first used, the duration of hearing aid use, and the hearing threshold. At the whole-brain level, we observed that AC-FC to different brain regions, primarily in the occipital lobe, but also in posterior middle temporal gyrus (**Figure S3A**), are influenced by the age at which our deaf participants began using hearing aids, such that higher FC is correlated with older ages of onset. Interestingly, there was no correlation between the duration of hearing aid use and AC-FC with any brain region (no significant clusters, $p < .05$, cluster-corrected for multiple comparisons). Last, we tested the correlation between AC-FC and hearing threshold. This analysis was possible only on a subset of our sample ($N = 23$), with the remaining participants only able to report the level of hearing loss (i.e., 'profound') rather than specific hearing threshold values, and therefore should be interpreted cautiously. We found that AC-FC to the left fusiform gyrus is correlated with the hearing threshold of deaf participants (**Figure S3B**), indicating that more profound hearing loss is associated with stronger FC between the AC and the fusiform gyrus. Since these correlations did not implicate any of the areas we identified here as having higher AC-FC variability in the deaf (**Figure 1A, B**), we directly tested if the individual differences in AC-FC to these regions could be accounted for by these hearing-related parameters. We performed the same correlation analysis at the ROI level using individual clusters extracted from the map in **Figure 1A**. No significant correlations were found for any of the factors or ROIs (all $p > .05$ before correction for multiple comparisons, see **Figures S4**, **S5**, and **S6** for scatter plots of AC-FC and each individual factor). These findings suggest that while hearing experience factors such as



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hearing threshold and age of hearing aid use can influence AC-FC, they do not account for the observed increased variability observed in our study, underscoring the role of congenital deafness in increasing AC-FC individual differences.

Discussion

This study demonstrates 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. These were not driven by differences in their hearing threshold or hearing aid use experience, but rather by congenital auditory loss. This shows consistency with previous findings of increased individual differences in blindness (S). a Furthermore, there is a mild 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 significantly 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 language acquisition timing itself also plays an additional significant role in producing different AC functional connections. These findings suggest that although hearing loss 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

The results of this study also provide evidence for the role of neural plasticit in neratn iverse ind

	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	14.31 ± 2.31	15.09 ± 1.91	15.03 ± 1.93
Gender	11 M, 5 F	12 M, 11 F	15 M, 18 F

Table 1.

Participants' information.

questionnaire, with the following 4 options: hereditary (selected by N = 15), maternal disease (N = 4), ototoxicity (N = 9), and other/unknown (N = 11 wrote “unknown”). Note that we are unable to confirm the self-reported etiology of hearing loss due to the lack of medical records and the lack of systematic medical examinations for hearing loss in China twenty to thirty years ago. All deaf participants indicated severe (N = 8) or profound (N = 31) deafness from birth, except for three participants who reported becoming deaf before the age of 3. Self-reported hearing thresholds ranged from 85 to 120 decibels (dB). Some of the participants used hearing aids during their lifetime, however, speech comprehension was reported as very poor, even when hearing aids were employed. At the time of testing, five deaf participants were using hearing aids frequently (either daily or 3-4 times per week); one reported to have used hearing aids, only but rarely (1-2 times per month); while others either had never used hearing aids or had used them for varying durations (with usage spanning from 0.5 to 20 years, see also **Table S2**). Only one deaf participant reported having received long-term oral training from teachers starting at age 2.

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. 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 ($p > .34$).

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 nuisance variable in our FC analyses, and the differences in variability were assessed after statistically accounting for the age variable.

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 or 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

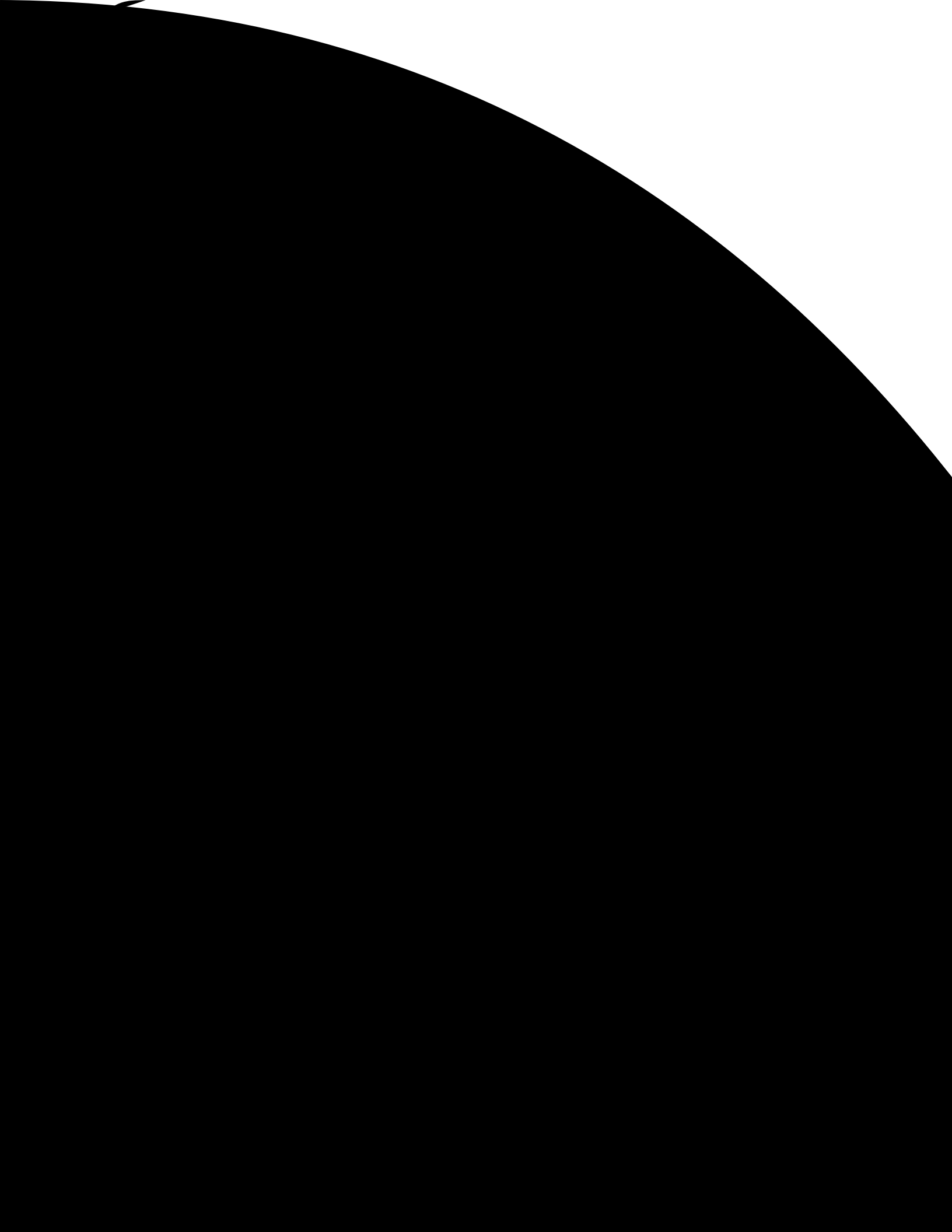
n & o Forsythe test (B F) is a homogeneity of variance test like Levene's test, conventionally used to test for variability differences, but uses the median instead of the mean, safeguarding against false positives in cases of skewed data distribution (K O). i The regression of the age variable was implemented in the analyses comparing deaf vs. hearing (given the age difference between these groups), while the regression of task variables (i.e., accuracy and reaction times) was included in all analyses to account for task performance effects. The minimum significance level for all presented results was established at $p < .05$, cluster-corrected for multiple comparisons within the gray matter volume using the spatial extent method (a set-level statistical inference correction, F l e o , Fl a). i a 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). This analysis was replicated for additional control ROIs – including all ROIs from the Harvard-Oxford Atlas not related to audition or language, and the number of significant voxels was calculated per ROI to test if the change in variability in deafness is specific to the AC. To determine if the number of voxels in AC was significantly higher than in the other control ROIs, we conducted a chi-square test for goodness of fit (**Figure S1**).

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 n Hearing, **Figure 1B** ; (S)) 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 hearing loss (deafness) or from late exposure to language. To test the role of hearing loss, 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**).

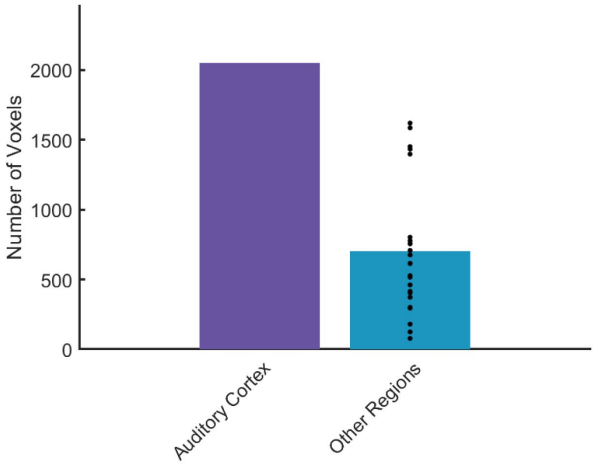
In addition to the variability analysis, FC data was also analyzed to directly compare the connectivity between the groups, with a one-way ANOVA (**Figure 2A**). To inspect the direction of reorganization in AC-FC, we computed a post hoc t-test comparing FC between the groups (deaf vs. hearing, **Figure 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. To ensure the additional smoothing step does not introduce artificial correlations, we also calculated the significance level without applying Gaussian smoothing to the permuted maps. 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**).

Co e l r a t i o n x p v i e t h e h e a r i v a g i a

In order to inspect the effect of specific factors related to hearing experience (see also **Table S2**) on AC-FC variability, we calculated the correlation between the AC-FC of each voxel for deaf participants and: 1) hearing threshold, defined as the lowest dB across both ears (numeric value available for 23 participants); 2) hearing aid use start age, for 28 participants who reported having used hearing aids; 3) hearing aid use, for all deaf participants, except one who did not report the exact length of use for the hearing aids (N = 38). These correlations were computed at the whole-

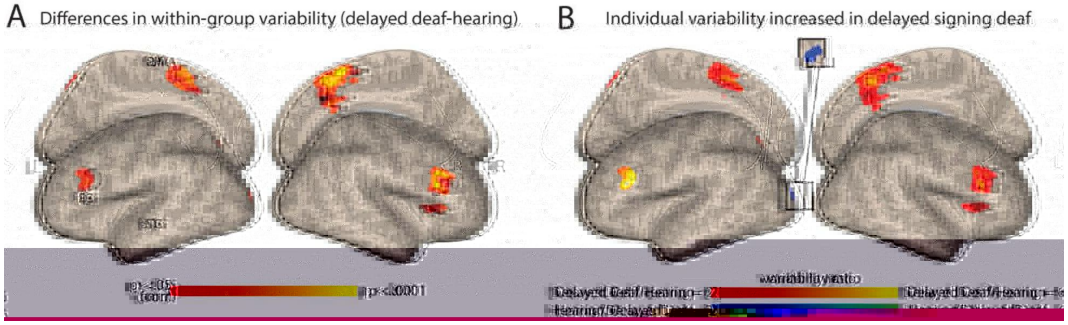


Supplementary Figure



Supplementary Figure

Auditory cortex functional connectivity (AFC) variability differences between delayed signing deaf and



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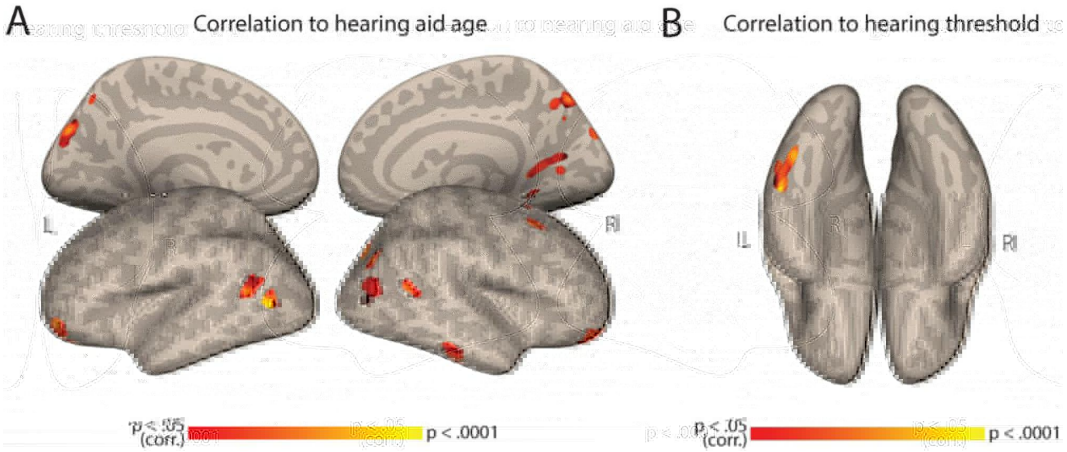

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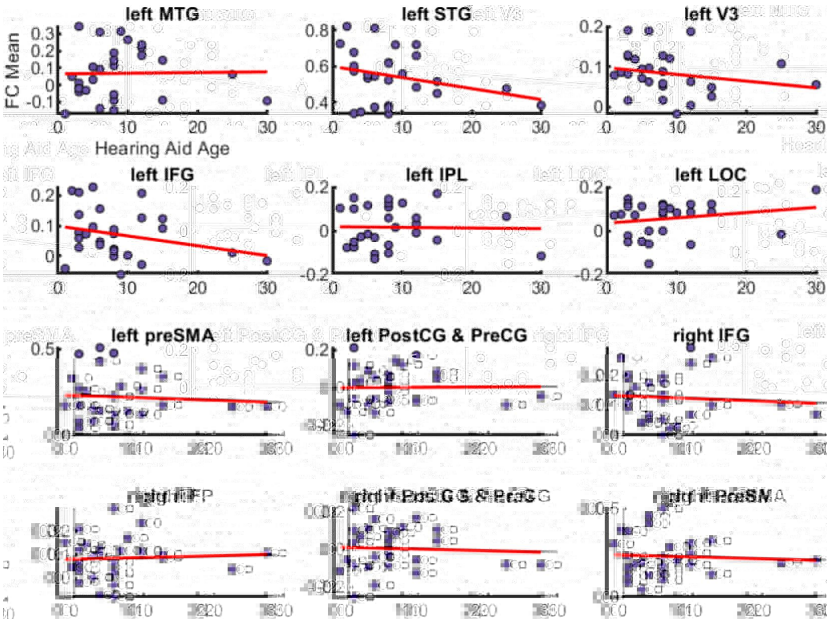

S u p p l e mee n 5t .a r y Fi g u r

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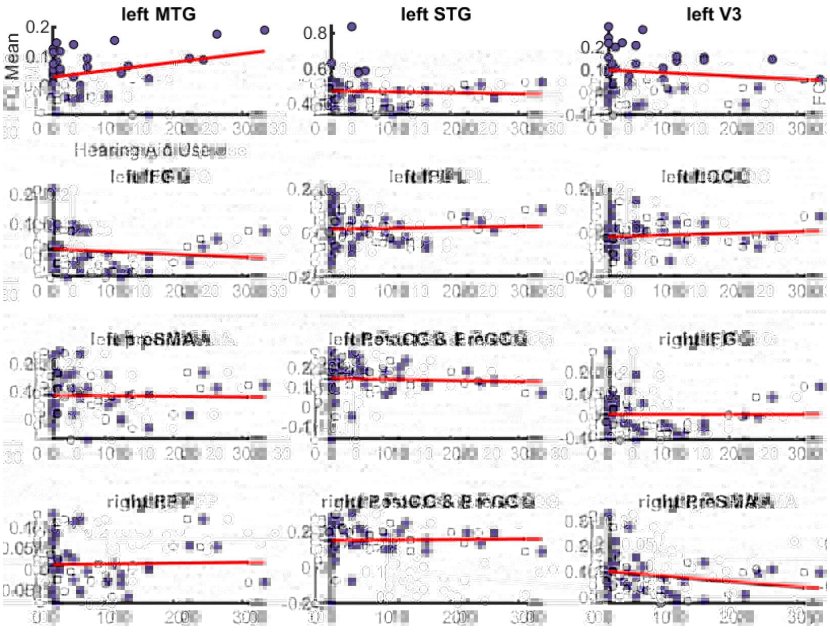

Supplementary Figure 6

Scatter plots at individual participant level showing the relationship between functional connectivity (FC) and hearing aid use. Each dot represents the mean value of FC and hearing aid use for one participant.

		Deaf vs. Hearing (peak F-value) Fig. 1A	Deaf Native vs. Hearing (peak F-value) Fig. 1C	Deaf Delayed vs. Hearing (peak F-value) Fig. 3D	Deaf Delayed vs. Deaf Native (peak F-value) Fig. 3A
Left Hemisphere	*Superior Temporal Gyrus*	-56 -16 4 (15)	-64 -28 0 (15.7)		
	Middle Temporal Gyrus	-64 -44 0 (16.3)	-56 -46 2 (17.2)		
	Inferior Frontal	-40 20 24 (15.5)	-46 28 20 (30.4)	-40 20 24 (13.2)	

Supplementary Table 1. MNI coordinates (x, y, z) for the FC variabi

Subj no.	Age	Age (months)	Sex	Years of education	Age of deafness (months)	Hearing loss-left ear (dB)	Hearing loss-right ear (dB)	Age of sign language acquisition	Hearing aid use	Age of hearing aid	Hearing aid use duration (years)
34	15	20	female	12	15	110	110	7	used in the past	3	22
35	16	27	male	12	15	100	100	5	uses currently	3	27
36	14	22	female	11	14	110	110	9	used in the past	9	22
37	14	23	female	11	14	71-90	71-90	8	used in the past	15	23
38	12	22	male	12	12	120	120	8	never used	-	22
39	12	22	male	>90	12	>90	>90	10	never used	-	22
40	15	23	male	71-90	15	71-90	71-90	9	used in the past	15	23
41	19	24	male	>90	16	>90	>90	7	never used	-	24
42	15	23	female	71-90	15	71-90	71-90	4	uses currently	12	23
43	14	22	female	11	14	71-90	71-90	8	used in the past	9	22
44	18	24	female	11	16	105	105	7	uses currently	22	24
45	19	20	female	11	12	>90	>90	8	used in the past	14	20
46	24	24	male	11	16	95	95	5	used in the past	8	24
47	31	31	male	11	16	100	100	8	never used	-	31
48	42	42	male	11	16	95	95	7	used in the past	3	42
49	39	39	male	11	16	100	100	5	used sporadically	10	unknown
50	31	31	female	11	16	>90	>90	5	used in the past	20	31
51	34	34	female	11	16	71-90	71-90	5	used in the past	10	34
52	33	33	male	11	16	100	100	9	used in the past	5	33
53	25	25	female	11	16	110	110	8	uses currently	4	25
54	30	30	male	11	16	>90	>90	8	never used	-	30
55	30	30	male	11	16	100	100	5	used in the past	10	30
56	21	21	male	11	15	100	100	0	used in the past	10	21
57	23	23	male	12	15	120	120	0	never used	-	23
58	23	23	male	12	15	120	120	0	used in the past	4	23
59	23	23	male	>90	14	>90	>90	0	used in the past	8	23
60	28	28	female	>90	15	>90	>90	0	never used	-	28
61	39	39	female	90	16	110	110	0	never used	-	39
62	21	21	male	90	12	90	90	0	never used	-	21
63	37	37	female	85	15	85	85	0	used in the past	1	37
64	22	66	0	20	22	male	120	0	used in the past	2	0
65	34	67	0	0	34	male	100	0	uses currently	31	0
66	30	68	0	10	30	female	110	0	used in the past	4	0
67	44	69	0	>90	44	male	>90	0	used in the past	0.5	0
68	25	70	0	0	25	male	90	0	used in the past	0.5	0
69	22	71	0	10	22	male	110	0	never used	-	0
70	12	72	0	>90	>90	female	105	0	used in the past	>90	0

Supplementary Table 2. **Additional characteristics of deaf participants.**

References

What was the Hominin Last Shared Ancestor like?
Current Anthropology 2020

Neuroanatomical correlates of handedness in primary motor, dorsal premotor, and language cortices between hearing signers
Frontiers in Neuroanatomy 2014

Compensatory plasticity and sensorimotor recruitment of the horizontal semicircular canal
Journal of Physiology 2014

Visual Illusions Reveal Neural Representations of Action Capacity
Psychological Science 2016

Overlapping but dissociable substrates of gaze adaptation and saccade programming
Brain 2014

Hemispheric asymmetries in the streuscturial connectivity of the human brain
Journal of Neuroscience 2014

Lingitudinal stability of barin plasticity
Nature Academy Science Bulletin 2021

Adaptive synaptic modulation via an intracellular modulatory variant
Academy Science 2014

Rieglocarnizagtei-oscarciand fenelbtarworks in adult to se of hexanidnitfeogrmayonticizoumtainelgndéafh
Neurogcnoa 2016

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Deafness and Connexin Expression in Porcine Cochlea
Porcess sai Mrgcrcg 2021

Functional development of early
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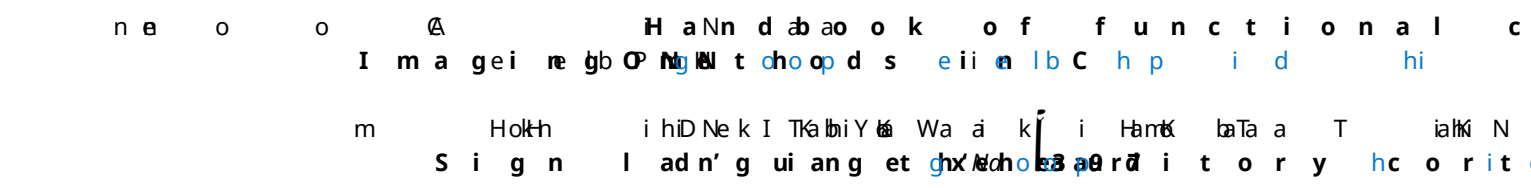

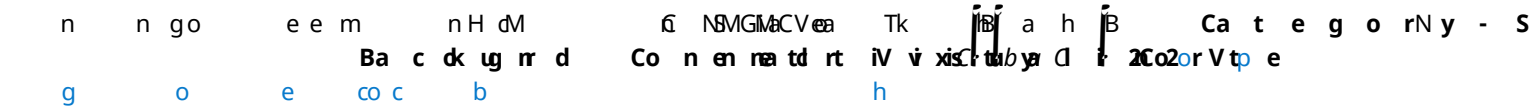

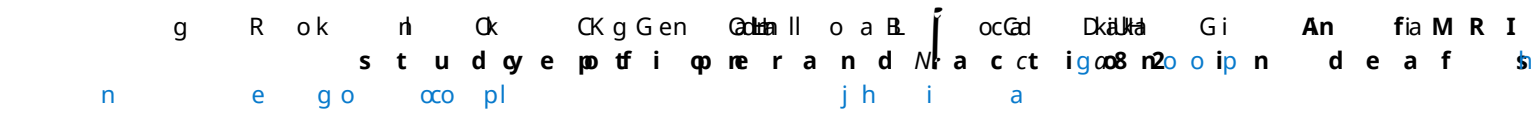

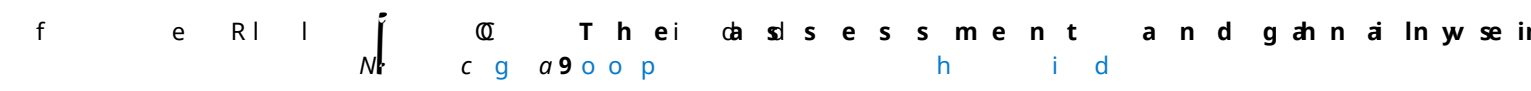

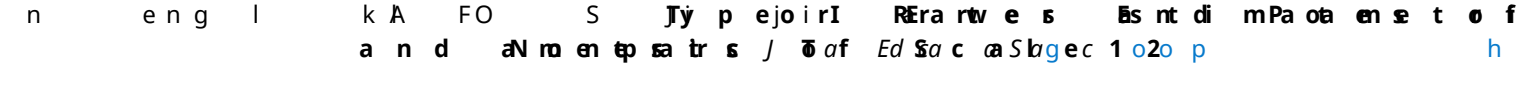

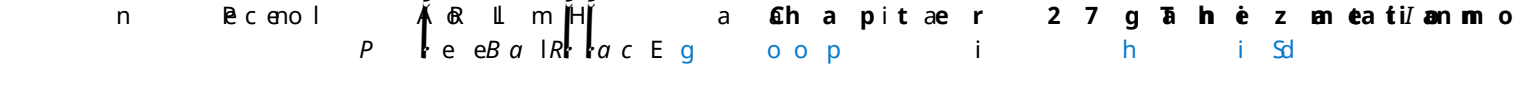

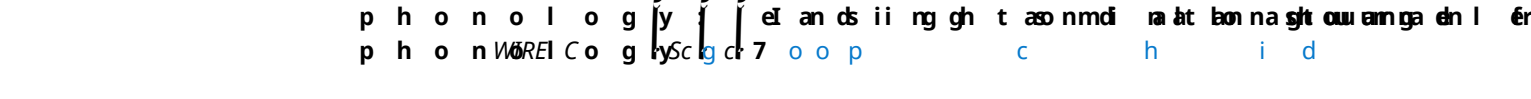

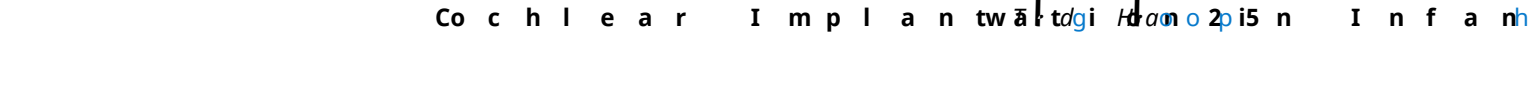

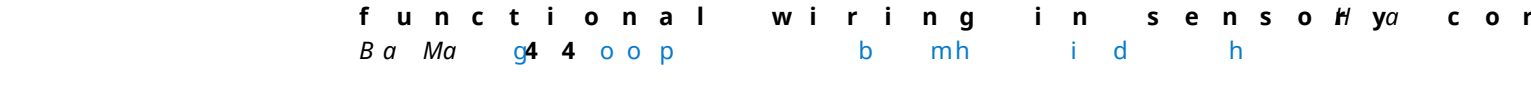

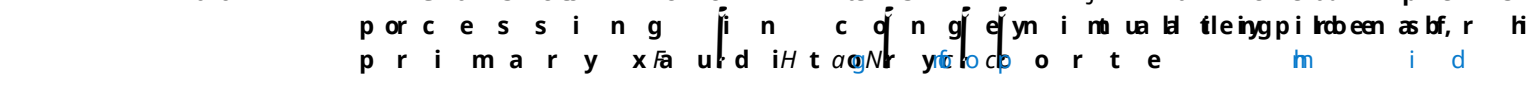

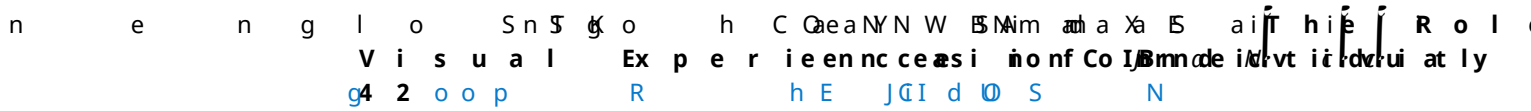

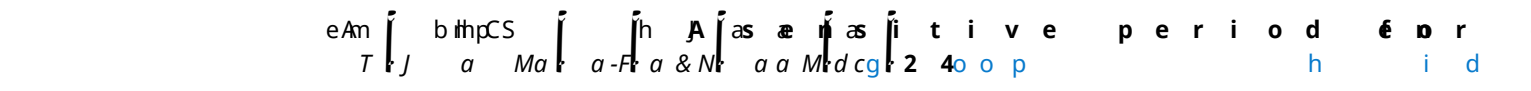

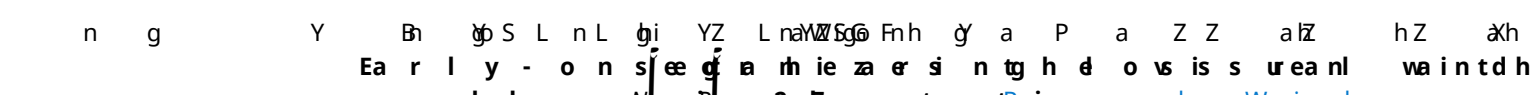

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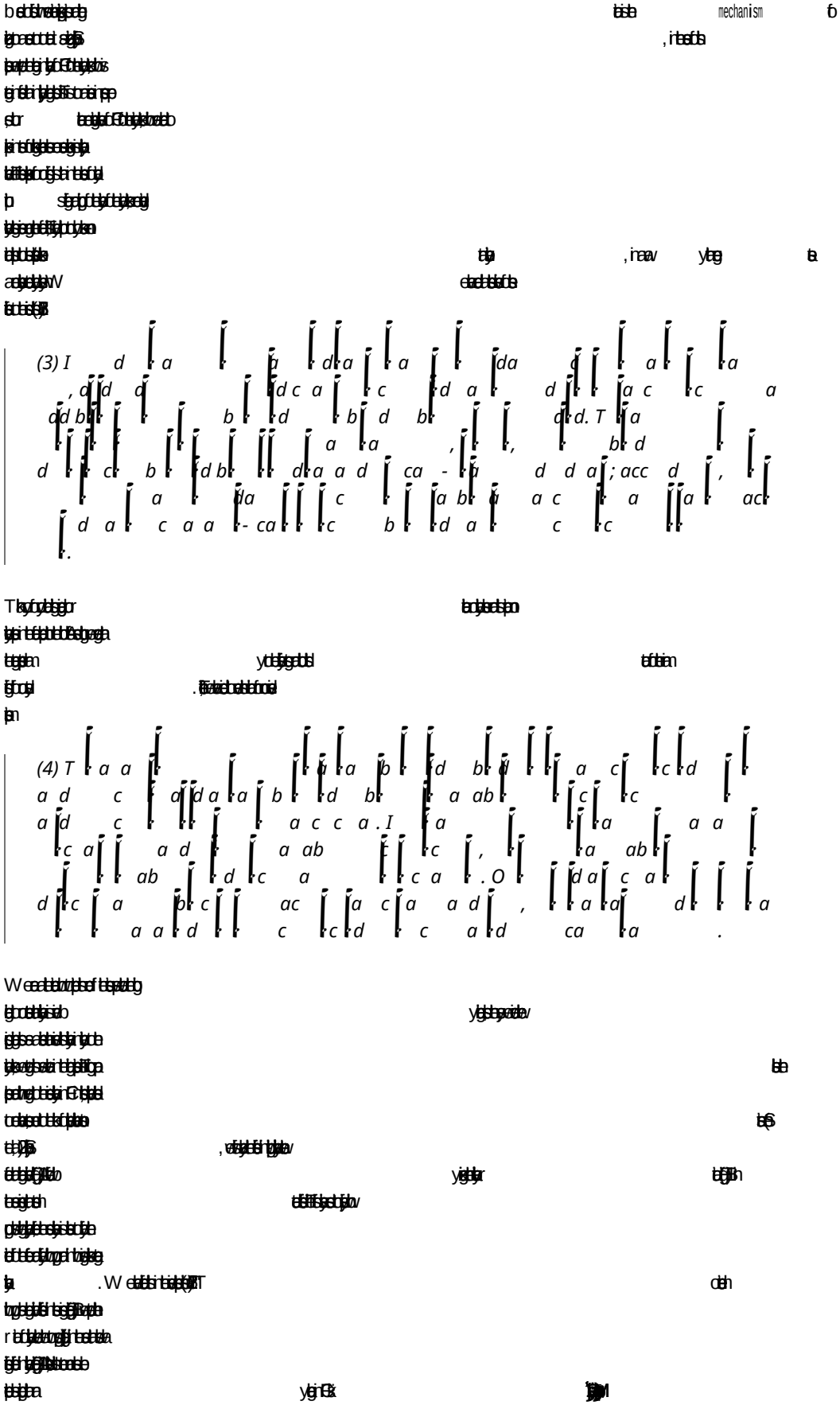

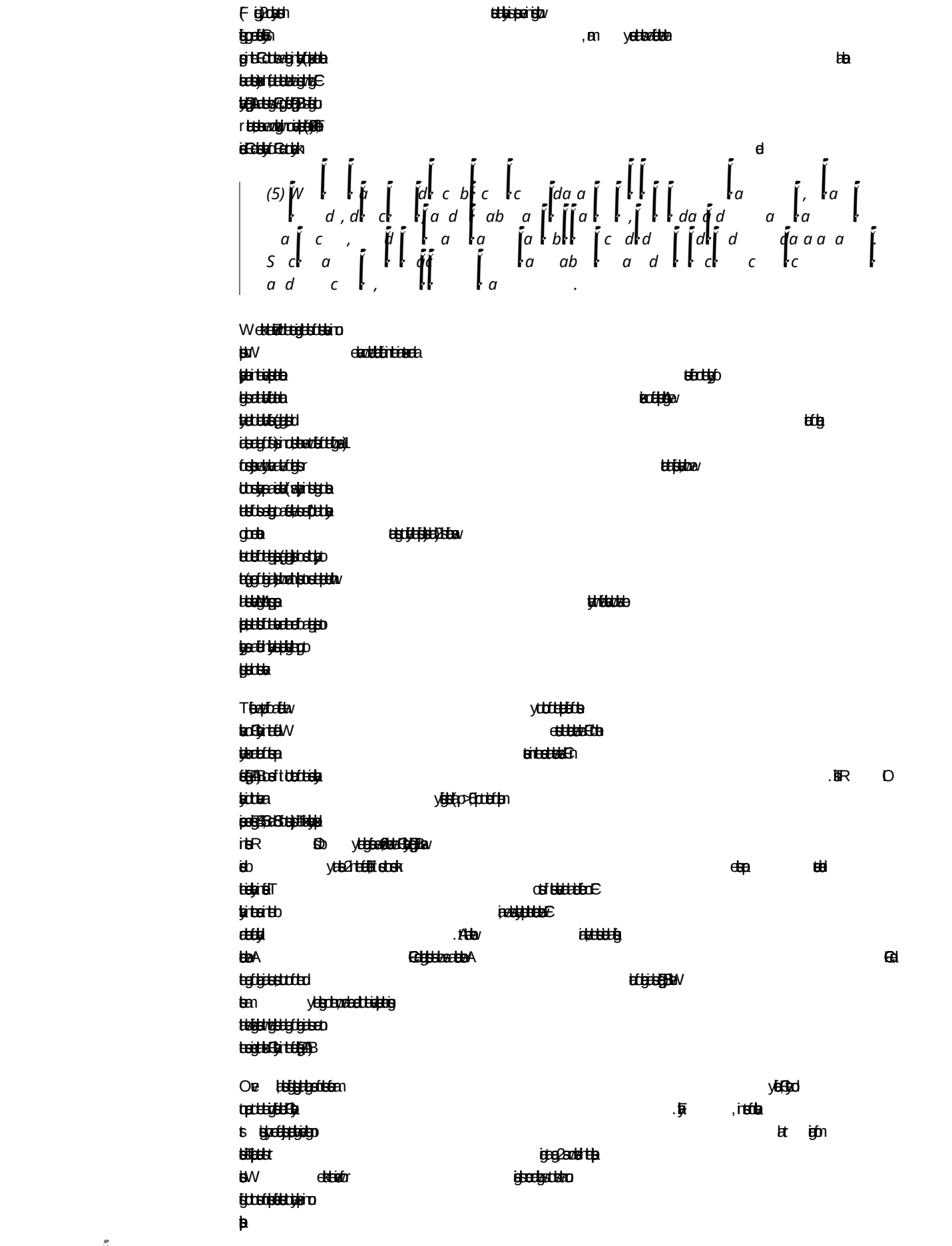

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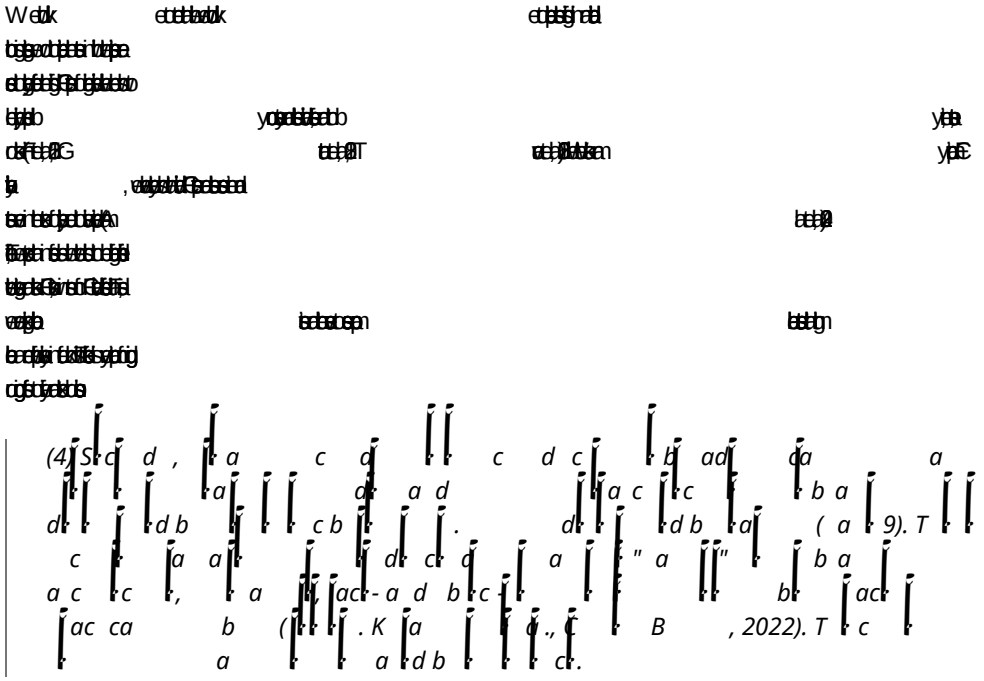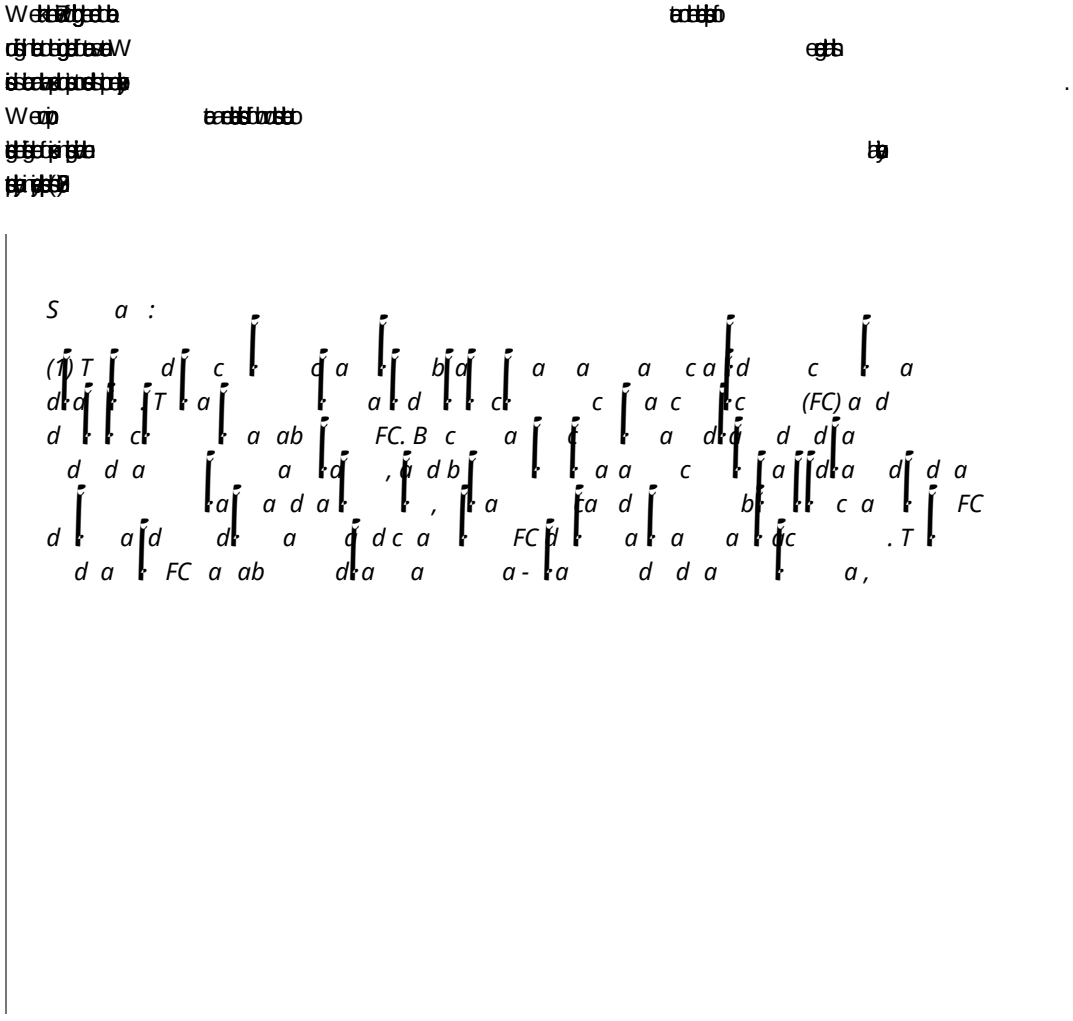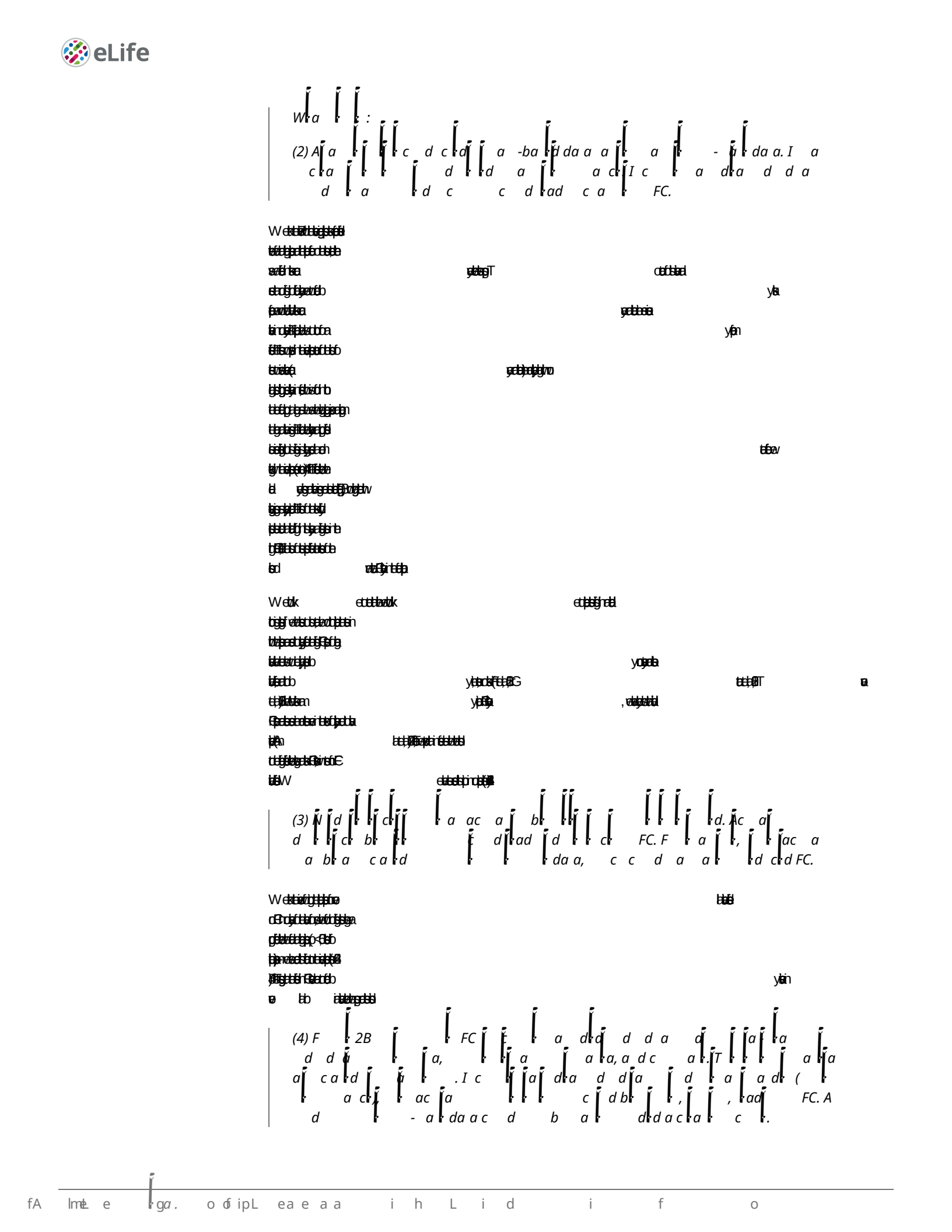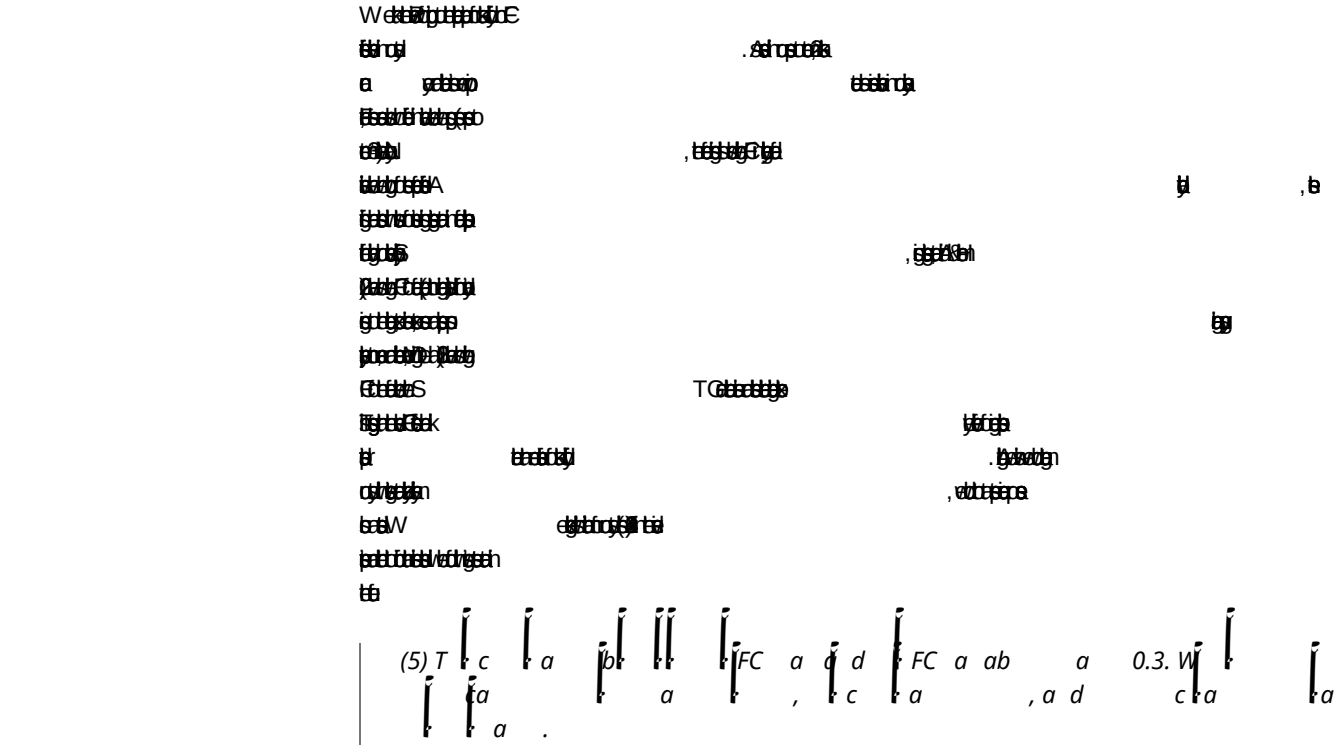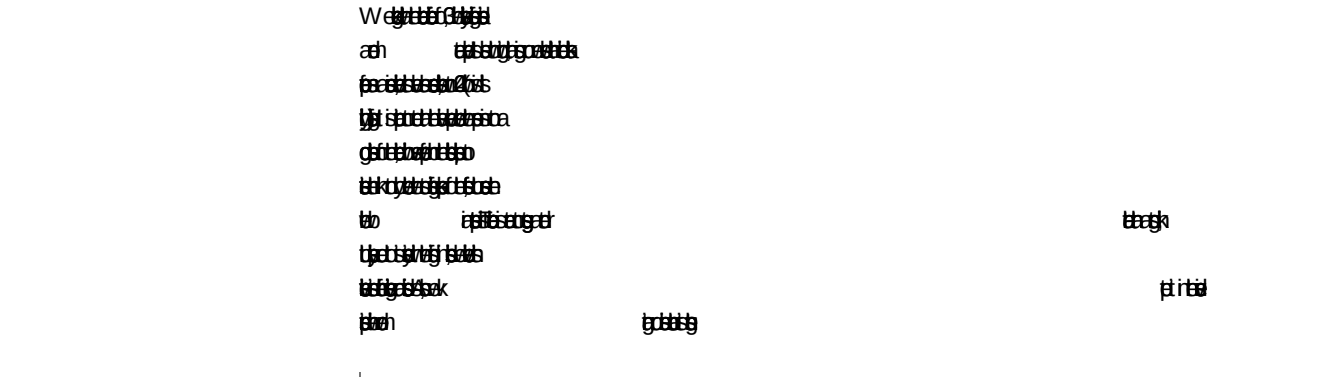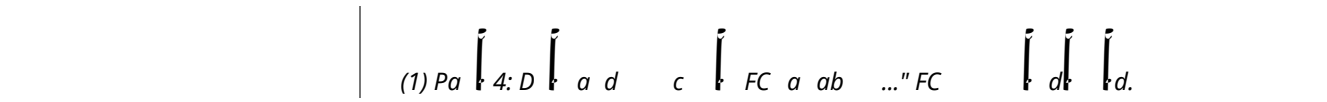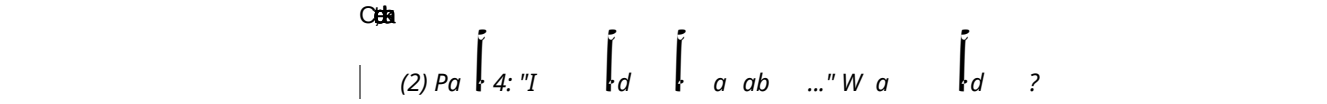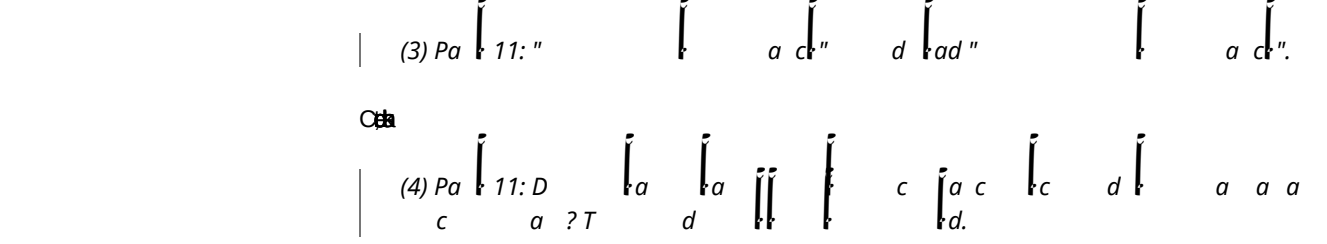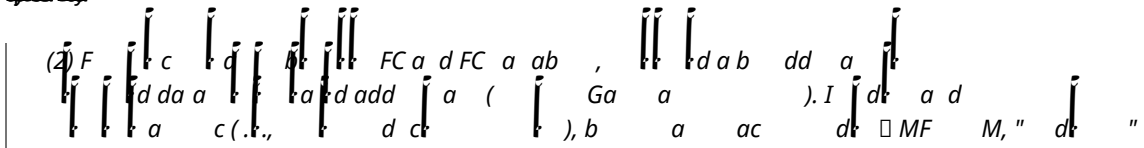
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