

Auditory areas are recruited for naturalistic visual meaning in early deaf people

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Auditory areas are recruited for naturalistic visual meaning in early deaf people.

Maria Zimmermann, Jagiellonian University; Rhodri Cusack, Trinity College Dublin; Marina Bedny, Johns Hopkins University; Marcin Szwed, Jagiellonian University

ABSTRACT

Early deafness enhances responses of auditory cortices to non-auditory tasks, yet the nature of the reorganization is not well understood. Here, naturalistic stimuli were used to induce neural synchrony across early deaf and hearing individuals. Participants watched a silent animated film in an intact version and three versions with gradually distorted meaning. Differences between groups were observed in higher-order auditory cortices in all stimuli, with no significant effects in the primary auditory cortex. Comparison between levels of scrambling revealed a heterogeneity of function in secondary auditory areas. Both hemispheres showed greater synchrony for the intact movie than for low-level variants. However, the right hemisphere showed an increased inter-subject synchrony for the low-level movie variants, which was not present on the left. An event segmentation validated these results: the dynamics of the right secondary auditory cortex unfolded as shorter length events with more transitions than the left. It also uncovered a further left-right asymmetry: Only left-hemisphere patterns matched the patterns of the hippocampus, a brain region situated at the top of cortical hierarchy. Our results reveal how deaf subjects use their auditory cortex to process visual meaning.

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28 INTRODUCTION

29

30 Studies of sensory loss provide insights into mechanisms of plasticity in the human brain.
31 Following deafness, auditory cortices become responsive in a wide range of non-auditory tasks.
32 These include perceptual tasks, such as peripheral vision (Finney et al., 2001), motion
33 perception (Scott et al., 2014; Shiell et al., 2016), visual motion discrimination (Benetti et al.,
34 2021a) and temporal and spatial sequence processing (Bola et al., 2017; Zimmermann et al.,
35 2021). Responses have also been found to various high-level functions, including working
36 memory and executive control (Andin et al., 2021; Cardin et al., 2018; Twomey et al., 2017)
37 (Manini et al., 2021).

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39 Despite clear evidence of functional reorganization, many questions remain unanswered about
40 the extent and nature of plasticity. A central issue is whether different parts of the auditory
41 network are recruited for different cognitive functions in deafness. In hearing people, there is
42 a clear and consistent organization within and across hemispheres (Wessinger et al., 2001;
43 Zatorre et al., 2002). Within hemisphere, there is a hierarchy of processes. Primary auditory
44 cortices are involved in low level perception, secondary process higher level auditory stimuli,
45 and the STS more involved in multimodal processes including meaningful narrative
46 processing. There is also specialization across hemispheres with the left hemisphere being more
47 engaged in processing speech, and the right being more involved in processing non-verbal
48 auditory stimuli (Albouy et al., 2020; Belin et al., 1998). The degree of specialization in the
49 auditory system of people born deaf remains unclear. Do different parts of the auditory cortices
50 take on different functions? How much of the auditory cortices show deafness-related changes
51 and do these changes extend into primary as well as secondary auditory cortices?

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53 Such questions about the level of processing and the anatomical extent of the repurposing have
54 been difficult to tackle using traditional task-based fMRI studies. Each experiment typically
55 tests a specific cognitive process and targets a specific part of the auditory cortex that responds
56 to the function in question. For example, several studies have failed to find any responses in
57 primary auditory cortices (e.g. Bola et al., 2017; Cardin et al., 2018), but it is not known
58 whether this is simply because these studies happened not to have sampled the particular
59 processes to which A1 responds in deafness.

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To get a more coherent and broader picture of the extent and nature of auditory cortex repurposing, we apply a complementary approach: data-driven analyses with naturalistic meaningful stimuli, i.e., an animated movie (Hasson et al., 2004). The basic tenet of this approach is that a rich, continuous stimulus, such as a story or a movie, captures a wide swath of cognitive processes levels, from low-level sensory perception to high-level narrative construction (Hasson, 2004; Hasson et al., 2008; Lerner et al., 2011). Data-driven analyses methods can then be used to gain insight into the level of processing that maximally applies to a given cortical system. One such method quantifies inter-subject synchronization for an intact animated movie and for gradually distorted variants of the same film, to assess which broad level of cognitive functions a particular area supports. Previous studies have found that low-level sensory regions (e.g., primary auditory and visual cortices) generally exhibit similar levels of synchronization for intact and disrupted versions of the stimulus, with only a small decrease in synchrony with greater distortion. Higher level regions, in contrast, show a steep synchronization drop when the meaning is removed scrambling or the temporal structure of the movie is distorted (Hasson et al., 2004, 2008). In the current study, we used this approach to test whether across areas of auditory cortices there is variation in the fall off synchrony with distortion. If so, this would suggest that auditory areas differ in their position in the cognitive processing hierarchy (Hasson, 2004; Hasson et al., 2008; Lerner et al., 2011).

In a second approach, we used Hidden Markov Models (HMM) to derive the underlying temporal structure of the neural response to the intact animated movie across cortical areas (Baldassano et al., 2017). This approach models neural activity as a series of discrete steady states separated by boundaries. Previous studies have found that higher-level regions (e.g., precuneus, PFC, hippocampus) lock into longer steady states corresponding to high-level processing of a meaningful narrative. By contrast, low-level perceptual regions (early sensory areas, such as V1) show shorter steady states, even for highly meaningful and complex stimuli such as movies (Baldassano et al., 2017; Cohen et al., 2022; Lee et al., 2021) HMM also makes it possible to directly match event boundaries across cortical areas. Regions performing analogous functions should not only parse the stimulus into similar size events, but also show event boundary alignment among these events.

HMM and inter-subject correlation analyses are complementary. Both provide insight into the level of processing within the cortical hierarchy but HMM analysis uses a different principle

94 and relies solely on data from the intact meaningful movie stimulus. Consistent evidence from
 95 these two approaches would provide clear insight into the level of processing across different
 96 auditory regions.

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98 RESULTS

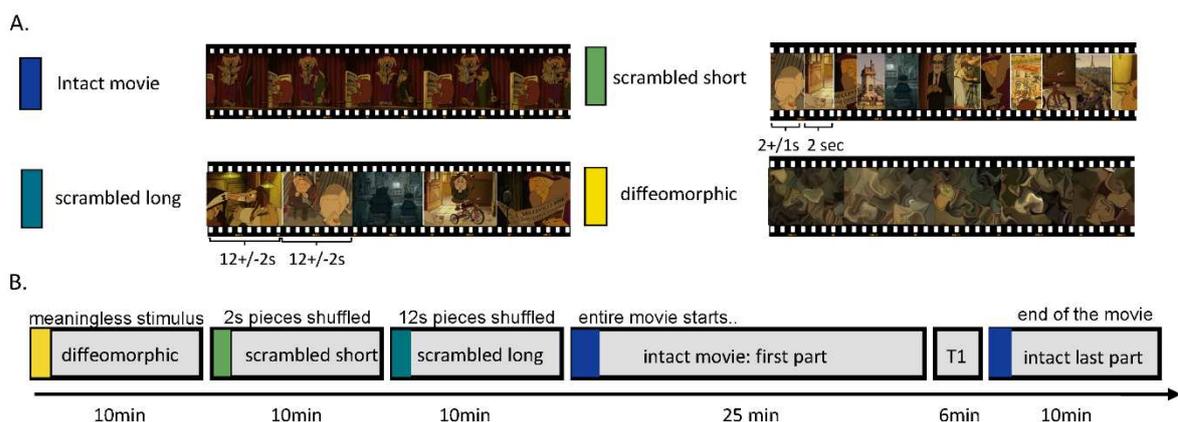
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100 To measure functional reorganization in auditory cortices and determine their position in a
 101 putative processing hierarchy, we measured cortical activity with fMRI while deaf and hearing
 102 participants viewed an animated silent movie (“The Triplets of Belleville”) as well as several
 103 distorted variants of the same movie: long scramble (12-second chunks, scrambled in temporal
 104 order), short scramble (2 second chunks, scrambled) and visually distorted (frame-by-frame
 105 diffeomorphic warping) version that removed meaningful content (e.g., objects) but preserved
 106 the low-level visual characteristics of the movie (see Fig..1).

107

108 The original version of the movie does not include any language but did include music. In our
 109 study, the soundtrack was removed to match the experience as much as possible across deaf
 110 and hearing participants. We performed inter-subject correlation analysis separately in each
 111 group, for each of the three distorted versions of the movie, and on 10 minutes of the intact
 112 movie.

113 FIG.1



114

115 Fig.1. (A) Stimuli: Participants passively watched an animated silent movie (“The Triplets of Belleville”) in one intact and three
 116 distorted versions (prepared of the last 10 minutes of the intact movie): (1) scrambled long (dark green) (2) scrambled short
 117 (light green) (3) diffeomorphic (yellow): visually distorted version, prepared by applying diffeomorphic image transformation
 118 to the intact movie. (B) Design: Three modified versions of the movie were first presented in counterbalanced order, followed
 119 by the first part of the intact movie (blue) (25 minutes). This was followed by an anatomical scan, after which the last part of
 120 the intact movie (green) (10 minutes)

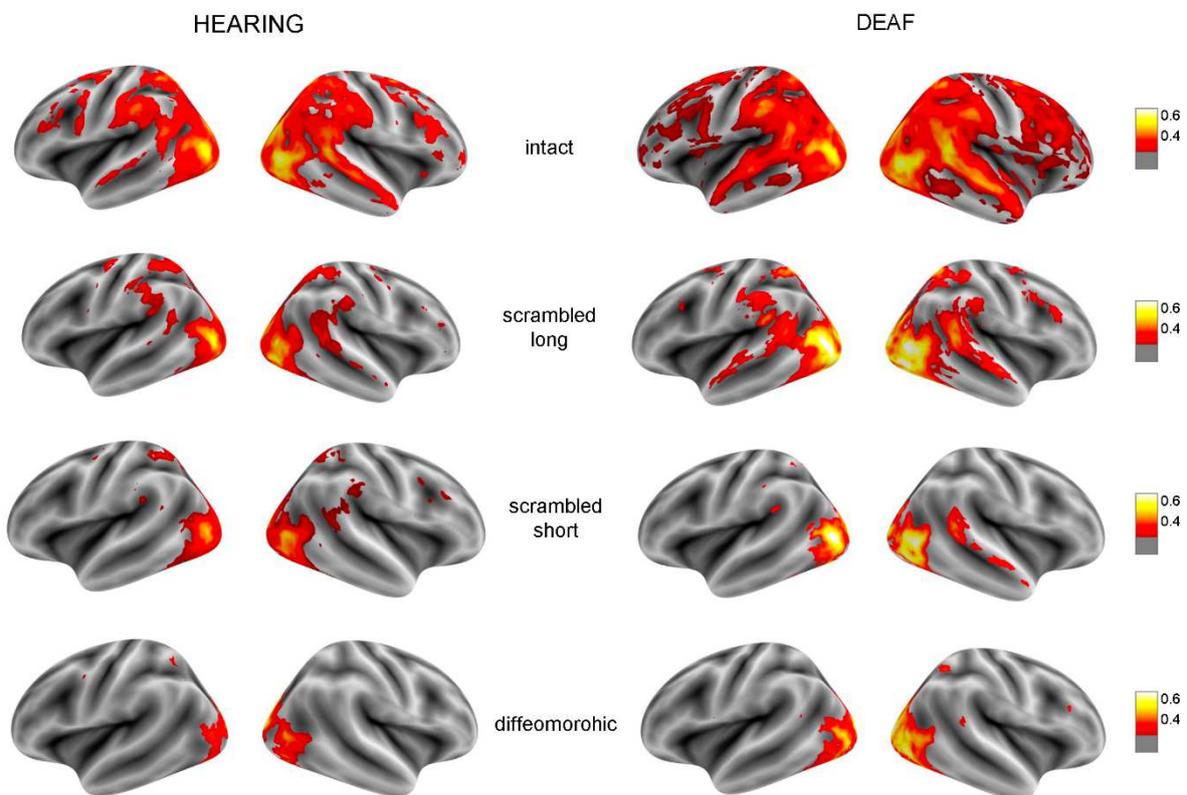
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122 *Increased synchronization of auditory cortices in deafness*

123 We found increased synchrony for the animated film in the deaf group in a range of higher-
124 order auditory areas, in bilateral superior and middle temporal cortices (Fig. 2; see Fig. S3 for
125 all between-groups contrasts). Increased synchrony in the deaf group was also observed in
126 secondary visual cortices. Interestingly, no between group differences were observed in
127 primary auditory cortex of either hemisphere, suggesting lack of reorganization of this region
128 for vision or visual semantics.

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FIG.2



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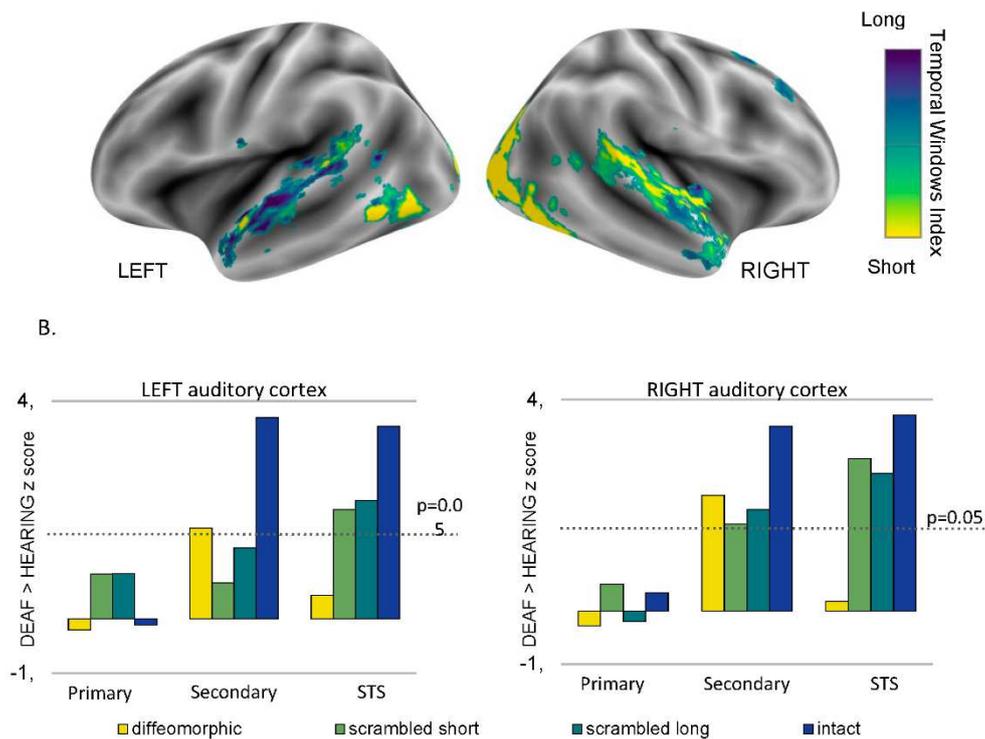
132 Fig.2. Whole brain Inter-subject correlation maps, shown separately for each stimulus type and each group (deaf and
133 hearing). Results show the hierarchy of cognitive processing in both group: early visual cortices were synchronized to a similar
134 degree across stimulus types, while higher-cognitive areas are more synchronized by the intact version. The significance was
135 calculated using nonparametric permutation tests. The maps represent ISC significant at the level $p < 0.05$ FDR voxel wise
136 corrected

137

138 Comparison across levels of scrambling revealed heterogeneity of function across different
139 secondary auditory areas within and across hemispheres in the deaf group (Fig. 3A). For all

140 vertices that showed an increase synchrony in the deaf relative to the hearing group, we
 141 calculated a Temporal Receptive Window (TRW) Index, which estimates the slope of
 142 synchrony decrease from the intact, most cognitively rich stimulus, to the scrambled and
 143 diffeomorphic, and least cognitively rich stimulus (calculated as: $z\text{-ISC}_{intact} * 3 + z\text{-ISC}_{scrambled\ long} - z\text{-ISC}_{scrambled\ short} - z\text{-ISC}_{diffeomorphic} * 3$). This analysis revealed that
 144 left secondary auditory cortices showed a steeper slope than the right, suggesting a higher order
 145 of processing in the left hemisphere. The TRW also varied within the right hemisphere along
 146 the medial to lateral and posterior to anterior axes. In both hemispheres, the superior STS
 147 (STS1), a higher order auditory region in the hearing, showed the highest temporal receptive
 148 windows index in the deaf group. More superior, earlier auditory areas showed shorter
 149 receptive windows. This pattern was most pronounced in the right hemisphere.
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FIG.3 A.



152
 153 Fig.3. (A) Regions with significantly higher synchronization in the deaf versus hearing coloured with Temporal windows:
 154 yellow represents short temporal windows, blue - long temporal windows. Left hemisphere audio cortex in the deaf show
 155 higher temporal windows and right hemisphere show both lower and higher temporal windows (B) Deaf > Hearing ISC
 156 differences: effects sizes (z-scores) for four auditory ROIS (primary Te1, secondary Te2, higher Te3 and STS)
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159 Region of interest (ROI) analysis comparing responses across hemispheres, auditory areas
160 (primary, secondary and STS), groups and levels of scrambling, likewise revealed a
161 heterogeneity of function in the deaf group. Importantly, the effect of group interacted with the
162 effect of hemisphere and the stimulus type (interaction: group x hemisphere x stimulus type
163 ($F(1,1,3) = 5.96, p < 0.01$), suggesting that the left and right auditory cortex in the deaf exhibit
164 different inter-subject correlation patterns and may operate on different levels of processing.
165 In the deaf group, there were also differences in levels of processing across auditory areas
166 within hemisphere, since the effect of group also interacted with ROI and with stimulus type
167 (interaction: group x ROI x stimulus type ($F(1,2,3) = 3.69, p < 0.01$)).
168 Consistent with the whole-brain analyses, an ROI analysis looking specifically in primary
169 auditory cortex found no significant synchrony in this region in either group for any stimulus
170 type. In sum, comparison of synchrony across different levels of scrambling and distortion
171 revealed functional differentiation across and within hemispheres in the deaf group.

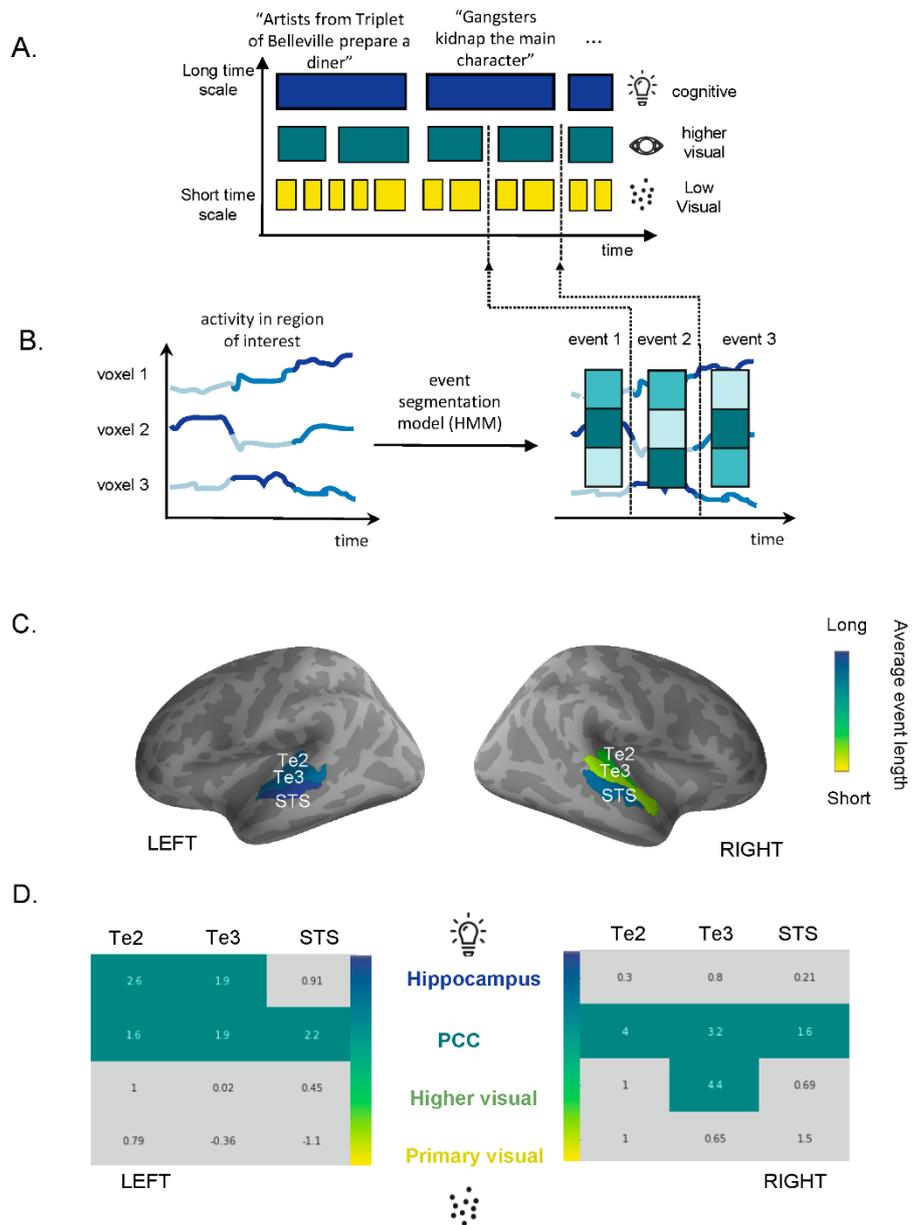
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173 *Data-Driven Event segmentation of naturalistic movie with Hidden Markov Model*

174 We next performed an event segmentation analysis on a partly independent data, a longer
175 movie stimulus (25 minutes) using Hidden Markov Model (HMM) (Baldassano et al., 2017).
176 This analysis uses HMM to detect neural event boundaries and characterize the temporal
177 structure of neuronal dynamics occurring while subjects were watching the intact movie (Fig..
178 4A-B, see methods). This approach revealed results consistent with above comparisons across
179 different levels of scrambling in the ISC analysis. Consistent with the idea that deafness leads
180 to recruitment of auditory cortices for processing of visually meaningful stimuli, in the deaf,
181 HMM models were well fitted bilaterally for the area of the superior temporal sulcus (STS1)
182 and in the two regions of secondary auditory cortex (Te2 and Te3) (Fig.. 4C), whereas in the
183 hearing the fit was significant only in the right STS. Notably, the fit was not significant in
184 primary auditory cortex of the deaf group, consistent with lack of synchrony in this region in
185 the ISC analysis.

186

187 The HMM analysis also revealed heterogeneity of the level of processing across auditory areas
188 in the deaf group. In the left secondary auditory areas of the deaf participants, HMM identified
189 longer (fewer) events (30 events), while in the right higher-level auditory cortex, the events
190 were shorter and more numerous (70 events) (see Fig.. 4C). Within hemispheres, the superior
191 STS showed fewer and longer events (right, left) relative to more superior secondary auditory
192 areas in the STG (right, left).



193

194 Fig.4 (A) Exemplary depiction of events (segments) in the movie (B) Schematic depiction of the event

195 segmentation method (C) Preferred number of events in the auditory cortex ROIs in the deaf. Plots represents

196 the auditory ROIs in which significant HMM models were matched ($p < 0.05$, corrected). Preferred number of

197 events in the auditory cortex ROI in the deaf (two regions in the secondary auditory cortex and STS) white outline

198 represents the primary auditory cortex. (D) Events match between auditory ROIs and four chosen ROIs

199 representing different hierarchy levels. Significance of the match was calculated using permutation test.

200 Numbers represent effect sizes (z-scores), significant between ROIs alignment were marked green.

201

202 Notably, HMM event segmentation can derive not only the number of these segments, but also

203 the timing of the transitions between them. In previous studies, better alignment between

204 regions has been demonstrated for areas close to each other in processing hierarchy
205 (Baldassano, et al 2017).

206 We found that both left and right auditory cortex align with higher level regions including
207 prefrontal cortex, precuneus, posterior cingulate cortex, and attention related regions including
208 SPL and IPS. However, only the right hemisphere secondary auditory areas to align with lower-
209 level, secondary visual regions, while only the left hemisphere aligned significantly with
210 hippocampus (Fig.. 4D, Fig.. S5). This additionally supports the claim of a right and left
211 secondary cortices are situated in different places in the processing hierarchy.

212

213

214 DISCUSSION

215

216 We found that secondary auditory areas early deaf people engaged in extracting visual meaning
217 from a naturalistic animated movie. When watching a silent movie, secondary but not primary
218 auditory cortices synchronized significantly more in deaf than hearing individuals and became
219 less synchronized as the meaning of the stimulus was distorted by scrambling. Data-driven
220 event segmentation using a Hidden Markov Model revealed a coherent event structure in
221 secondary ‘auditory’ cortices of deaf people at slow and intermediate timescales. These two
222 lines of evidence suggest that in everyday situations, deaf people use their secondary auditory
223 cortices to extract visual meaning from rich non-verbal stimuli. These findings from naturalistic
224 stimuli, compliments previous task-based studies and provide an organizing principle for
225 several studies of task-related activations previously observed across the auditory cortex.

226

227 The responses to the naturalistic film and its distorted variants revealed functional segregation
228 across different auditory areas in deafness. As the meaning of the movie was progressively
229 disrupted by temporal and spatial scrambling, the left hemisphere showed a sharper fall-off in
230 synchrony, relative to the right. Data driven HMM analysis likewise showed longer processing
231 time-scales in the left hemisphere, with slower event transitions. This result suggests a higher-
232 order level of processing in left than right hemisphere auditory areas of deaf people, since these
233 respond maximally to high-level content at slower timescales and shower transitions in neural
234 states.

235

236 Heterogeneity was also observed *within* the hemispheres. HMM revealed slower event
237 transitions (~1-minute events) in more lateral STS regions bilaterally, while the secondary

238 auditory areas of the right hemisphere (Te2, Te3) unfolded at a faster timescale (~.20 second
239 events) and showed a less steep decrease in synchrony with scrambling. Overall, we found
240 clear evidence of functional segregation in auditory areas, with different auditory regions
241 engaged at different levels in the cognitive hierarchy and recruited in different ways for process
242 visual meaning in deafness.

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247 *Primary auditory cortex of the deaf is 'silent' during visual processing*

248
249 The rich and multifaceted naturalistic stimulus used in our study did not evoke a significant
250 response in the primary areas in the hearing or the deaf group. This means that A1 is not
251 involved in any of the broad range of different visual semantic and perceptual functions
252 engaged in processing of an animated movie. The lack of A1 recruitment in deafness contrasts
253 with the plasticity observed in congenital blindness, where the primary visual cortex shows
254 robust activations for a range of cognitive tasks, including naturalistic auditory movies and
255 stories (Sadato et al, 1996, Loiotile et al., 2019; Van Ackeren et al., 2018). The lack of A1
256 recruitment is particularly interesting in the context of the current debate regarding the
257 reorganization of primary auditory regions in deafness and is consistent with multiple possible
258 interpretations.

259

260 One possibility is that the repurposing of the auditory cortex does extend to primary auditory
261 regions, but the relevant functions were not captured by watching an visual film. The few
262 studies with deaf participants that did show activations in the primary auditory cortex of the
263 deaf involved fast executive processing, such as task-switching (Manini, et al., 2021) and
264 double flash detection (Karns et al., 2012). In the current study, the movie was viewed
265 passively. Karns et al. (2012) also observed that primary auditory area somatosensory
266 responses were stronger than visual responses. Thus, it is also possible that A1 is recruited by
267 somatosensation, also not captured in the current study. This hypothesis is supported by animal
268 studies showing the recruitment of A1 for somatosensory sensing in deaf cats (Hunt et al.,
269 2006; Meredith & Lomber, 2011), as well as studies on plasticity in the cochlear nucleus, which
270 shows an increase in the number of somatosensory projections after auditory deprivation
271 (Shore et al., 2007; Zeng et al., 2012).

272

273 Another possibility is that A1 in the deaf does not get reorganized and remains functionally
274 dormant. In this scenario, the cross-modal plasticity in the deaf stops at the boundaries of the
275 secondary auditory cortex in the posterior part of the superior temporal gyrus (STG) (Cardin et
276 al., 2020). In fact, activations of the primary auditory cortex in the deaf induced by visual or
277 tactile tasks are generally modest or absent. Various tasks, including language (MacSweeney
278 et al., 2004), visual semantic task (Twomey, et al. 2017) working memory (Cardin et al. 2018)
279 face recognition (Benetti, et al. 2017), visual motion perception (Benetti, et al. 2021) and tactile
280 and visual sensory discrimination (Bola, et al. 2017, Zimmermann, et al. 2021) fail to evoke
281 activation in A1. Analogously, the primary auditory cortex in the deaf cat also does not show
282 effects of cross-modal reorganization (Kral et al., 2003, 2017). It is thus possible that primary
283 auditory areas in the deaf do not assume any new non-auditory functions. Indeed, animal
284 studies report an atrophy of the deep layers of the auditory cortex of deaf cats which disrupts
285 long-range connections, restricting communication with higher-order auditory areas (Berger et
286 al., 2017; Kral et al., 2017). If such atrophy exists in humans, it could preclude repurposing.
287 Anatomical post-mortem and high-field quantitative MRI are needed to verify this hypothesis.

288

289 *Heterogeneity across hemispheres*

290 We found clear evidence of differences in functional specialization of high-level auditory areas
291 in deaf people. The current finding of heterogeneity between auditory areas of the hemispheres
292 is consistent with previous studies showing that higher-level tasks, such as sign language and
293 working memory, can evoke greater activation in the left superior temporal cortex (STC) in
294 deaf participants (Cardin et al., 2013, 2018; Emmorey et al., 2011; MacSweeney et al., 2004)
295 while visual motion, spatial and lower-level processing evoke greater activation in the right
296 STC (Fine et al., 2005; Sadato et al., 2005). Interestingly, studies with animals find no such
297 hemispheric specialization. In deaf cats, left and right secondary and primary auditory cortices
298 do not differ in response to visual (Lomber et al., 2010) or somatosensory stimulation
299 (Meredith & Lomber, 2011). This suggests that the lateralization in the temporal cortex in the
300 deaf may be unique for humans and could be related to evolutionary predisposition for
301 language and speech in the left hemisphere

302 In the hearing, the superior STS of the left hemisphere is maximally responsive to spoken
303 language and unresponsive to a wide range of non-linguistic tasks (e.g., visual working
304 memory, social and numerical reasoning) (e.g. Deen et al., 2015; Fedorenko et al., 2011).
305 However, recent evidence suggests that even in the hearing, non-verbal meaningful events

306 depicted in movies (Sueoka et al., 2022) and pictures (Ivanova et al., 2021) do engage language
307 systems in the STS and elsewhere, albeit less than language stimuli. Language regions might
308 therefore be poised to process meaningful events, whether conveyed by language or through
309 images and deafness enhances responses to visual meaning. The current findings suggest that
310 in deafness, responses to visual meaning also expand superiorly into secondary auditory areas,
311 which are thought to process lower-level aspects of speech in the hearing (H. Blank & Davis,
312 2016) Enhancement and expansion of responses to visual narratives in deafness could be
313 related to deafness per se, to different modalities of language use across hearing and deaf
314 populations, or both. Since linguistic processing in deaf signers is based on visuo-spatial
315 modality involving human motion and face expression, language areas in the temporal cortex
316 may enhance capacities to extract meaning from nonverbal visual narratives. Indeed, the
317 “Triplets of Belleville” plot is rich in various meaningful visual cues, social behavior, body
318 movement and gestures. In line with this interpretation, previous studies showed that deaf
319 signers show higher responsiveness to non-verbal meaning (gesture) in the left lateralized
320 auditory areas including the temporal cortex (Newmann, et al. 2015). In sum, more higher-
321 order processing of visual meaning in left than right lateral temporal cortices of early deaf
322 people may be related to intrinsic predispositions of these cortical areas for language in
323 humans.

324 A non-mutually exclusive possibility is that right secondary auditory regions might be taken
325 over by lower level visuo-spatial attention mechanisms. These mechanisms are known to be
326 right lateralized (Corbetta & Shulman, 2002). Task-based studies on deafness show significant
327 right posterior STG activations for several attention-related functions and perceptual tasks such
328 as spatial and temporal sequence discrimination (Bola et al., 2017; Zimmermann et al., 2021)
329 visual motion detection (Benetti et al., 2021), visuo- spatial working memory (Ding, et. al
330 2015).

331
332 Visually-driven attention is also right lateralized in the hearing and is usually associated with
333 regions proximal to superior temporal cortex, mostly the parietal junction (TPJ) (Corbetta &
334 Shulman, 2002; Geng & Mangun, 2011). In our data these right-hemisphere parietal areas, in
335 the deaf as well as in the hearing, show synchrony for the short-movie fragments (Fig.. 2). This
336 indicates that our short-fragment stimuli engage the type of attentional mechanisms in question.
337 The proximity of TPJ and temporal auditory areas, could then provide the basis for the
338 recruitment of the right STG (Te2, Te3) for spatial attention-related functions in the deaf. In

339 this scenario, the attentional functions based on the right TPJ would 'invade' its cortical
340 neighbors.

341

342 *Heterogeneity within hemisphere*

343

344 Our data also shows a hierarchy of processing within the auditory network of early deaf people.
345 Higher level regions in the lateral STS showed a steeper fall-off in synchrony and longer
346 processing time-scales in data-driven HMM analysis. The secondary auditory areas, in contrast
347 showed a shallower fall-off slope and shorter processing time-scales. The difference between
348 secondary auditory areas and more lateral STS regions was most pronounced in the right
349 hemisphere but also present in the left.

350

351 This divergence of functions between different regions of the higher auditory cortex in the deaf
352 is in part consistent with the cortical organization in the hearing. There is ample evidence that
353 regions in the STS are at least in part multimodal and engaged in processing non-verbal visual
354 meaning in the hearing population. The right STS responds to non-verbal components of a
355 narrative: face-voice matching (Campanella & Belin, 2007), gesture and face movement
356 (Rennig & Beauchamp, 2018) and meaningful biological motion (Puce & Perrett, 2003; Saxe
357 et al., 2004). This was also observed in the current data, where the right posterior STS shows
358 also significant synchronization in the hearing, and the HMM event segmentation revealed the
359 coherent event structure in this region in both groups. The structure of events in the right
360 posterior STS in deaf and hearing shows high consistency in the times when events occur. In
361 both groups, the right STS is likely to be engaged in processing higher level visual meaning,
362 with the stronger engagement in the deaf. The more unimodal part of the superior temporal
363 cortex, including STG (Te3, Te2) show coherent event structure only in the deaf and not in the
364 hearing.

365

366 This heterogeneity across different parts of the reorganized auditory cortex contrasts with the
367 findings in the blind. An analogous naturalistic stimuli study on the role of the visual cortex in
368 blind individuals showed that their primary visual cortex is synchronized exclusively for the
369 intact auditory movies (Loiotile et al., 2019). Unlike the current study in the deaf, this study
370 also found no evidence of a processing hierarchy differences across the visual cortices of
371 people born blind. These results suggest important differences in cross-modal reorganization
372 across different sensory systems.

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Conclusion

Using a rich naturalistic stimulus, we were able to capture the nature of auditory cortex repurposing across a range of different time scales and levels of meaning. Notably, both our analytical approaches, ISC and HMM, consistently showed the engagement of the auditory cortex in processing visual meaning in the deaf. The right hemisphere synchronized for both high- and low-level stimuli, while the left hemisphere specialized in higher-level narrative processing. In the right hemisphere, we found with secondary auditory regions involved in lower-level processing and shorter temporal windows, and right STS being engaged in higher-level processing. Overall, the heterogeneity of the auditory cortex in the deaf is at least partly consistent with specialization of temporal cortex in the hearing. These data suggest that in the absence of audition, secondary auditory areas become engaged in extracting meaning from visually presented events and subspecialize for different aspects of meaning extractions across and within hemisphere.

407

408 METHODS

409 *Participants*

410 21 early deaf participants (mean age= 31.7, SD= 5.4, 10 women) and 22 hearing participants
411 (mean age= 29.6, SD= 5.1, 10 women) participants took part in the study. Inclusion criteria for
412 deaf participants include prelingual deafness (onset of deafness < 8 months), severe level of
413 deafness (above 90dB threshold in both ears), and lack of a cochlear implant. All participant
414 data were analyzed in the stimuli-driven analysis (inter-subject correlation). One deaf
415 participant's data were removed from the second data-driven analysis, due to extensive head
416 movement. The control group consisted of 22 non-signers of hearing that matched the early
417 deaf signer group in age, level of education, and sex. All deaf participants reported acquiring
418 Polish Sign Language (PJM) as their first language. Ten participants reported having deaf
419 parents and acquired PJM (Polish Sign Language) from them as the first language, while 11
420 participants acquired PJM in early childhood (3-6 years old) as the first language.

421 For detailed information on deafness etiology and language experience, see Tables (Tables 1
422 and 2). Instructions were given orally for hearing and in Polish Sign Language (PJM) for deaf
423 participants (by use of a sign language interpreter). Written informed consent was signed by
424 all participants.

425 *Stimuli*

426 (1) Intact stimulus generated by shortening the *Triplets of Belleville* to 35 minutes by
427 removing scenes that were not directly relevant to the plot line.

428 (2) A piecewise scrambled version with long segments (12 seconds, +/- 2 seconds): The
429 movie was cut into chunks, and the segments were then shuffled and displayed in
430 pseudo-random order.

431 (3) A piecewise scrambled version with short segments 2 seconds (+/- 1 second): similar
432 to above, but with shorter segments.

433 (4) A diffeomorphic scrambled condition. A stimulus lacking any meaning was generated
434 by distorting the video using the diffeomorphic warping method (Stojanoski & Cusack,
435 2014). Unlike conventional methods for generating low-level control stimuli (phase
436 scrambling or texture scrambling), diffeomorphic warping preserves the basic
437 perceptual properties of the image while removing meaning. The diffeomorphic
438 stimulus is perceptually similar to the intact movie in terms of low-level visual features
439 regions (e.g., spatial frequency, spatial organization) and should yield similar response
440 in early visual

441 The modified versions were presented first in counterbalanced order. The intact movie
442 was displayed in two parts (25') and (10') always following the scrambled and
443 diffeomorphic conditions to ensure participants cannot derive any higher-level meaning
444 from lower level stimuli. (Fig.1).

445

446

447 *Data Acquisition*

448 MRI structural and functional data. MRI structural and functional data of the whole brain were
449 collected on a 3 Tesla Siemens MAGNETOM Tim Trio scanner. The T1-weighted structural
450 images were collected in 176 axial slices with 1 mm isotropic voxels using a magnetization -
451 prepared rapid gradient echo (MP RAGE). Functional images were collected using a gradient
452 echo planar imaging (EPI) sequence (36 sequential ascending axial slices, repetition time (TR)
453 1.4 seconds, echo time (TE) 30ms, flip angle 70°, field of view (FOV), matrix 76 x 70, voxel
454 size 2.5 x 2.5 x 2.5 mm, PE direction L/R. Data analyses were performed using fmriprep
455 (freesurfer), python (v. 3.7), the Brain Imaging Analysis Kit, <http://brainiak.org> (Kumar et al.,
456 n.d., 2020), Human Brain project siibra <https://siibra-python.readthedocs.io>, data analysis
457 toolboxes (nilearn, nltools) and Rstudio.

458

459 *Data Analysis*

460 *Preprocessing*

461 We performed minimal preprocessing using *fmriprep* (Esteban et al., 2019) the data have been
462 realigned and spatially normalized. After preprocessing with *fmriprep*, we smoothed the data
463 (fwhm=6mm) and performed voxel-wise denoising using a GLM. The six realignment
464 parameters, their squares, their derivatives, and squared derivatives were included. Additional
465 physiological and scanner artifacts were removed using linear, quadratic trends, and average
466 CSF activity.

467

468 *Whole-brain Inter-subject Correlation (ISC) Analysis*

469 The aim of this analysis is to evaluate the degree of stimulus-driven synchronization
470 (correlation) to that same voxel in other people's cortices. In the whole brain level analysis for
471 each voxel, the inter-subject correlation was calculated using the leave-one-out method. First,
472 voxelwise synchrony was calculated as the average Pearson correlation coefficient (r) between
473 the time course of one subject and the average time course of the rest of the experimental group
474 (Hasson et al., 2004; Lerner et al., 2011). This procedure was repeated for all subjects in a

475 group for each condition separately (intact, piecewise scrambled long, short, diffeomorphic)
476 Results were averaged across participants. The average ISC maps with values r were
477 transformed to Fisher's z values to allow comparisons of correlations between groups and
478 conditions. Differences in synchronization between stimuli and between groups were
479 compared by subtracting the relevant z -maps. Because ISC analysis violates the assumptions
480 required for parametric methods, we perform non-parametric hypothesis ISC testing using
481 permutation tests (Chen et al., 2016, 2017; Hasson, 2004; Lerner et al., 2011). A null
482 distribution was created by permuting the original data using the bootstrapping method. All
483 ISC whole-brain maps were thresholded at the level $p < 0.05$, FDR corrected voxel-wise, cluster
484 size > 20 voxels.

485 To investigate where different parts of the auditory cortex are located in the processing
486 hierarchy in the deaf population, we calculated the temporal receptive window index (TRW
487 index) for each region of the auditory cortex parcellation. To this end, we calculated differences
488 in synchronization between more meaningful and less meaningful stimulus types by calculating
489 a linear contrast across conditions ordered by degree of meaning. An analogous analysis was
490 previously performed by calculating the difference between synchronization for high and low
491 level stimulus (I. A. Blank & Fedorenko, 2019; Lerner et al., 2011). Here we additionally took
492 into consideration intermediate stimuli level, by subtracting all respective $zISC$ scores (e.g.
493 $zISC$ for the intact movie compared to $zISC$ for scrambled long stimulus, $zISC$ for scrambled
494 long compared to $zISC$ diffeomorphic, etc.) Adding all these differences together resulted in
495 the following. $TRW\ index = 3 * zISC\ intact + zISC\ scrambled_long - zISC\ scrambled_short -$
496 $3 * zISC\ diffeomorphic$. Note that, this linear contrast captures the first moment of the
497 differences and would be insensitive to higher order moments. To control for differences in
498 ISC between different parts of the brain the TRW indexes were normalized. For each voxel the
499 TRW index was divided by the highest $zISC$ score in this voxel.

500

501 *Controlling for the effect of stimuli order*

502 To investigate if there was an effect of “time-on-task”, we analyzed the synchronization elicited
503 by the first part (10 minutes) and the last 10 minutes of the intact movie. We found that the
504 first part of the intact movie led to significantly higher ISC than the last part of the movie (Fig..
505 2B). Led by this finding, we performed an additional control experiment to check whether the
506 difference between the level of whole- brain inter-subject synchronization evoked by different
507 parts of the movie comes from the effect of order or some inherent properties of different parts
508 of the film. Nine of the 22 hearing participants took part in this additional control fMRI

509 experiment. The first and last parts of the movie were presented in a counterbalanced order
510 (Fig. 1, supplementary). Additionally, we present the three control conditions that were
511 diffeomorphic and piecewise scrambled versions of the first part of the movie, in contrast to
512 the main experiment (Fig. 1), where the control conditions used the last part of the movie.

513 We found that the last part of the movie evokes a significantly lower inter-subject correlation
514 than the first part, even if controlled for the effect of order (Fig. 1). Critically, scrambled and
515 diffeomorphic versions of the first and last part of the movie evoked similar ISC levels. Given
516 these results, we decided to use the first part of the movie (first 10 minutes) as the main intact
517 stimulus in all subsequent analyzes. The results of an analogous analysis performed on the last
518 part of the intact movie are described in the Supplementary Material (Fig. S1)

519

520 *ROI analysis of inter-subject correlation (ISC).*

521 To compare the level of auditory cortex synchronization between subjects for different
522 conditions (stimulus types) between different parts of the temporal cortex, we proceed with the
523 ISC analysis on the temporal cortex parcellation (see ROI definition). We performed the ISC
524 analysis on anatomical ROIs. For each participant and each ROI, a time course was obtained
525 by averaging throughout the region. Similarly, as in the whole brain analysis, for each ROI,
526 each participant's ROI time course was correlated with the average ROI time course of all
527 participants in a group (deaf and hearing separately). The results were averaged among the
528 participants. The averaged ISC maps with r values were transformed to Fisher's z values. The
529 z-ISC values for each ROI were entered into the nonparametric permutation analysis of
530 variance (permANOVA) (Anderson, 2017) with four factors: group, ROI (3 levels: primary,
531 early, higher auditory cortex), hemisphere, and stimulus type (4 levels). This type of analysis
532 of variance allowed us to fit a multifactorial model to data that are not normally distributed: a
533 null distribution for each comparison was estimated using permutations (number of
534 permutations =10,000). Four main effects and two interaction effects were calculated (ROI x
535 stimulus type x group and hemisphere x stimulus type x group). We then performed *post hoc*
536 pairwise comparisons: we tested the difference between the groups for each of 3 ROI s and
537 four conditions (stimulus type) separately using nonparametric permutation tests (number of
538 permutations =10,000), p-values were adjusted for multiple comparisons using FDR
539 correction.

540

541 *Event segmentation using Hidden Markov Models*

542 Next, we proceed with a data-driven analysis of the intact movie data. For this analysis we used
543 larger portion of data: the first 25 minutes (first part, 1060 TRs) of the entire movie. We used
544 the larger portion of data in order to ensure enough power and test our hypotheses on partially
545 independent part of stimulus. The analysis assumes that when watching continuous stimuli
546 (movies), humans automatically divide the continuous stream of perception into segments. The
547 time scale of these segments may be derived from the brain signal for different regions of the
548 brain. This time scale should largely match the hierarchy of inter-subject correlation
549 coefficients revealed from the stimuli-driven approach explained above.

550 We performed HMM analysis on the auditory ROIs (STS1, Te3, Te2, Te1) defined from
551 Juelich atlas as well as in parcels throughout the cortex (Schaefer et al., 2018)

552 HMM models were estimated for each of the four ROIs separately. The number of events (i.e.
553 shifts in activation patterns) for each time series and each ROI was estimated using the Hidden
554 Markov model using *Brainiak HMM* module. We use the procedure for model fitting as
555 explained by Baldassano et al. 2017. First, the time course was obtained from each voxel of
556 the ROI (Baldassano et al., 2017) For each ROI, the event segmentation model was applied to
557 group-averaged data from all but one subject. We measured the robustness of the boundaries
558 by testing whether the event segmentation explained the temporal structure in the left-out
559 subject. We measured the correlation between all pairs of time points that were separated by
560 four time points and then sorted these correlations according to whether the pair of time points
561 was within the same event or crossed over an event boundary. The average difference between
562 the within-event versus across-event correlations was used to measure how well the learned
563 boundaries captured the temporal structure of the left-out subject. The analysis was repeated
564 for every possible left-out subject and for a varying number of events from $k=10$ to $k=90$. After
565 averaging the results across subjects, the number of events with the best within- versus across-
566 event correlations was chosen as the optimal number of events for this region. For the given k ,
567 the model was fitted for all but one subject. Finally, the structure of the event boundaries was
568 compared between ROIs of the temporal cortex and other brain structures: all 100 parcels and
569 hippocampus. We measured the match between these regions by computing the fraction of
570 boundaries in one ROI within three time points to boundaries in another ROI. The three time
571 points threshold was mean to adjust for a typical uncertainty in the model about exactly where
572 an event switch occurs is approximately three time points.(Baldassano et al., 2017)

573

574

575 *ROIs definition*

576 The auditory cortex ROIs were defined using the new Juelich, Human Brain Project
577 parcellation (Amunts et al., 2020; Zachlod et al., 2020). In both ROI analyses (ISC and HMM)
578 we used the ROIs located in the temporal cortex which are involved mostly in processing
579 auditory stimuli in the hearing population (Zachlod et al. 2020). These are 3 anatomically and
580 functionally distinct structures: one located along the Heschl gyrus (Te1.0, Te1.1 and Te1.2) –
581 primary auditory cortex, the second along the superior temporal gyrus –secondary auditory
582 cortex (Te2 and Te3) and the last in the superior temporal sulcus (STS1). In the HMM analysis,
583 the higher auditory cortex was further divided into secondary (Te2) and higher region (Te3) to
584 allow more fine-grain testing for a gradient. Both ISC and HMM analysis was also performed
585 in whole brain parcellation on 100 parcels (Schaefer et al., 2018) Additionally, we define the
586 hippocampus on the basis of the Juelich atlas.

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773 <https://doi.org/10.1523/JNEUROSCI.2527-20.2021>

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780 Tab.1.

	sex	age	education	level of deafness	onset of deafness	cochlear implant	hearing aids	how well do you hear speech using hearing aids
1	F	33	higher	> 120 dB	congenital	No	No	
2	M	37	higher	90- 119 dB	congenital	No	No	
3	F	36	higher	90- 119 dB	congenital	No	Sometimes	poor
4	M	32	higher	90- 119 dB	congenital	No	Yes	poor
5	M	29	vocational	90- 119 dB	5 months	No	No	
6	M	35	vocational	> 120 dB	congenital	No	No	
7	F	36	secondary	90- 119 dB	congenital	No	No	
8	M	23	secondary	> 120 dB	congenital	No	No	
9	M	27	higher	90- 119 dB	congenital	No	Sometimes	poor
10	M	34	higher	90- 119 dB	congenital	No	No	
11	M	26	higher	> 120 dB	congenital	No	Sometimes	poor
12	M	35	vocational	> 120 dB	congenital	No	No	
13	F	37	higher	90- 119 dB	congenital	No	No	
14	F	28	higher	> 120 dB	congenital	No	No	
15	M	31	secondary	> 120 dB	8 months	No	No	
16	M	34	higher	90- 119 dB	6 months	No	Yes	poor
17	M	39	secondary	90- 119 dB	congenital	No	Yes	moderate
18	F	21	higher	> 120 dB	congenital	No	No	
19	F	27	vocational	90- 119 dB	8 months	No	Yes	poor
20	F	21	higher	90- 119 dB	congenital	No	Yes	poor
21	F	33	higher	90- 119 dB	congenital	No	no	

781 Tab.1 Group of early deaf individuals: demographics

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785 Tab.2.

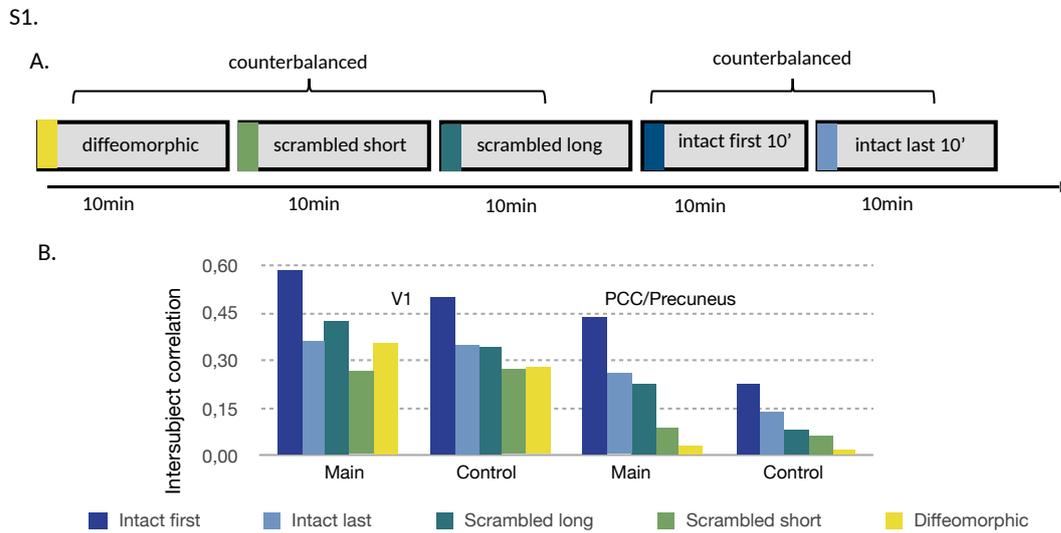
	deaf mother	deaf father	PJM native	how well do you understand polish speech?	how well do you speak polish	Polish Sign Language fluency	first language exposure	first language
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1	No	No	No	poorly	poorly	fluent	3-6 yo	PJM
2	No	No	Yes	moderate	poorly	fluent	3-6 yo	PJM
3	Yes	Yes	Yes	poorly	poorly	fluent		PJM
4	No	No	No	well	moderate	fluent	3-6 yo	PJM
5	No	No	No	poorly	poorly	fluent	3-6 yo	PJM
6	Yes	Yes	Yes	poorly	poorly	well		PJM
7	Nie	Yes	Yes	well	well	fluent		PJM
8	Yes	Yes	Yes	poorly	poorly	fluent		PJM
9	Yes	Yes	Yes	poorly	poorly	well		PJM
10	Yes	Yes	Yes	moderate	poorly	fluent		PJM
11	Yes	Yes	Yes	poorly	well	fluent		PJM
12	Yes	Yes	Yes	poorly	poorly	fluent		PJM
13	Yes	Yes	Yes	moderate	poorly	fluent		PJM
14	Yes	Yes	Yes	poorly	poorly	fluent		PJM
15	No	No	No	poorly	poorly	fluent	3-6 yo	PJM
16	No	No	No	moderate	poorly	fluent	3-6 yo	PJM
17	No	No	No	moderate	well	well	3-6 yo	PJM
18	Yes	Yes	Yes	poorly	poorly	fluent		PJM
20	No	No	No	moderate	moderate	fluent	3-6 yo	PJM
21	Yes	Yes	Yes	moderate	well	fluent		PJM
22	Yes	yes	yes	poorly	poorly	fluent		PJM

Tab.2 Group of early deaf individuals: language experience

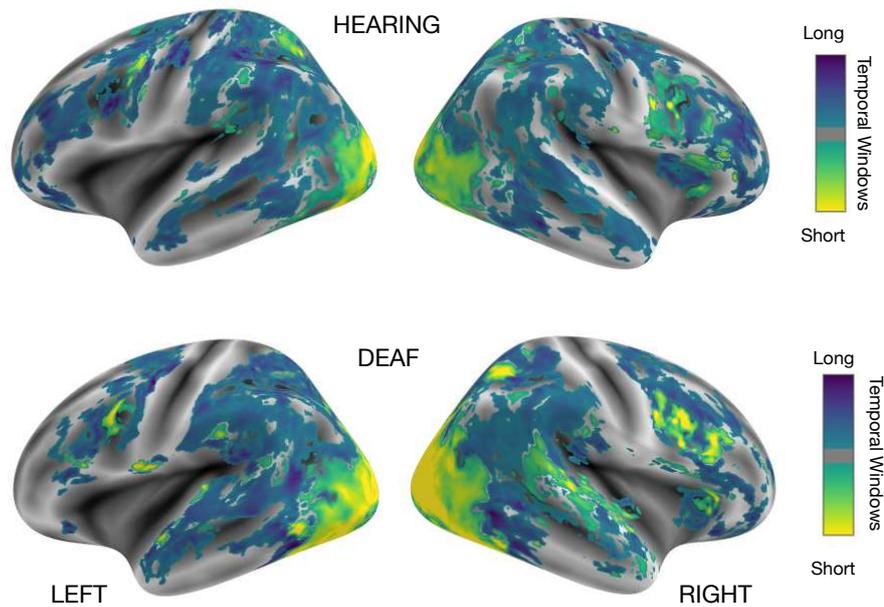
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 807 Supplementary Materials
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 811 Fig.S1. (A) Design of the control experiment. A control experiment was performed to test the effect of order and
 812 stimulus characteristics on the inter-subject correlation. Three modified versions of the first 10 minutes of the
 813 entire movie were presented (counterbalanced order) followed by the first and last part of the movie
 814 (counterbalanced order) (2) Results: the last part of the movie (green) lead to a significantly lower inter-subject
 815 correlation than the first part (blue), even if controlled for the effect of presentation order. Modified versions of
 816 the first and the last part of the movie (yellow, red, purple) evoked similar levels of ISC.
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S2.



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820 S2. Temporal receptive window analysis of the inter-subject correlations for the intact movie vs. scrambled
821 versions of the movie. The linear contrast was calculated by subtracting relative inter-subject correlation maps
822 : $TRW\ index = 3 * intact + long - short - 3 * diffeomorphic$. Lower values (yellow) indicate the preference for processing
823 scrambled/ modified version (short temporal windows). Higher values (dark blue) - more prevalent in the left
824 hemisphere - indicate the preference for processing the intact stimulus. Lower values (yellow) more represented
825 in the right hemisphere indicate the lack for strong preference for intact stimulus. Maps show voxels with ISC
826 higher than $r = 0.1$ for any condition.

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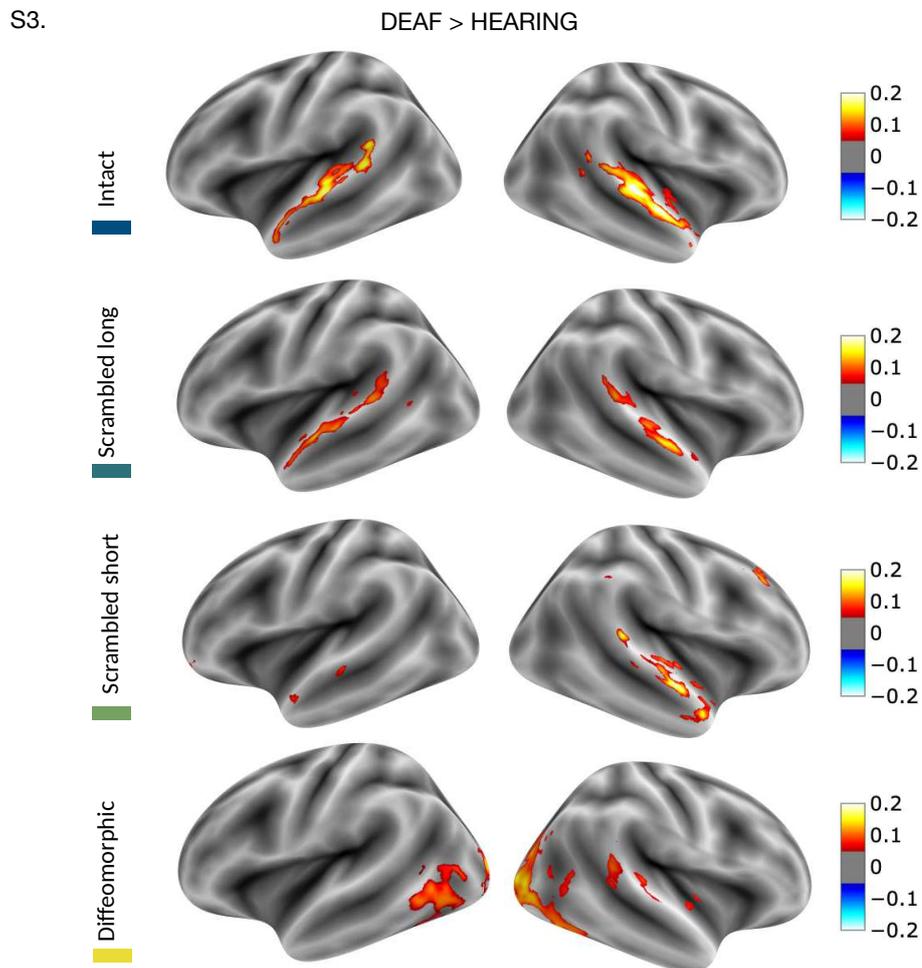
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844 S3. Regions with stronger inter-subject synchronisation in the deaf relative to the hearing. Stronger
 845 synchronization is seen in the secondary auditory cortex (STG) in the deaf for each stimuli type. The effect is
 846 bilateral for higher level stimulus (intact, scrambled long) and right lateralised for lower-level stimuli (scrambled
 847 short, diffeomorphic) Intergroup contrast was calculated using permutation bootstrapping test. Maps represent
 848 voxels significant at level $p < 0.05$ corrected for multiple comparisons using FDR.

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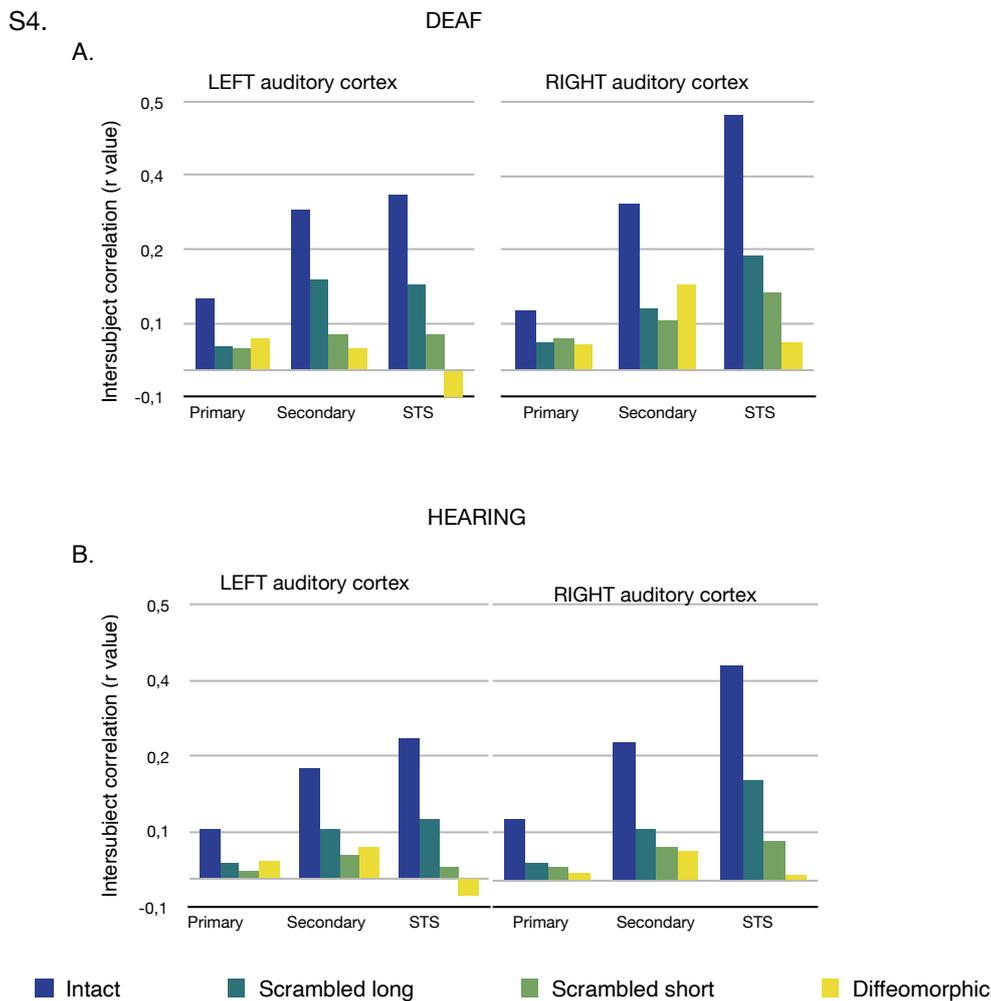
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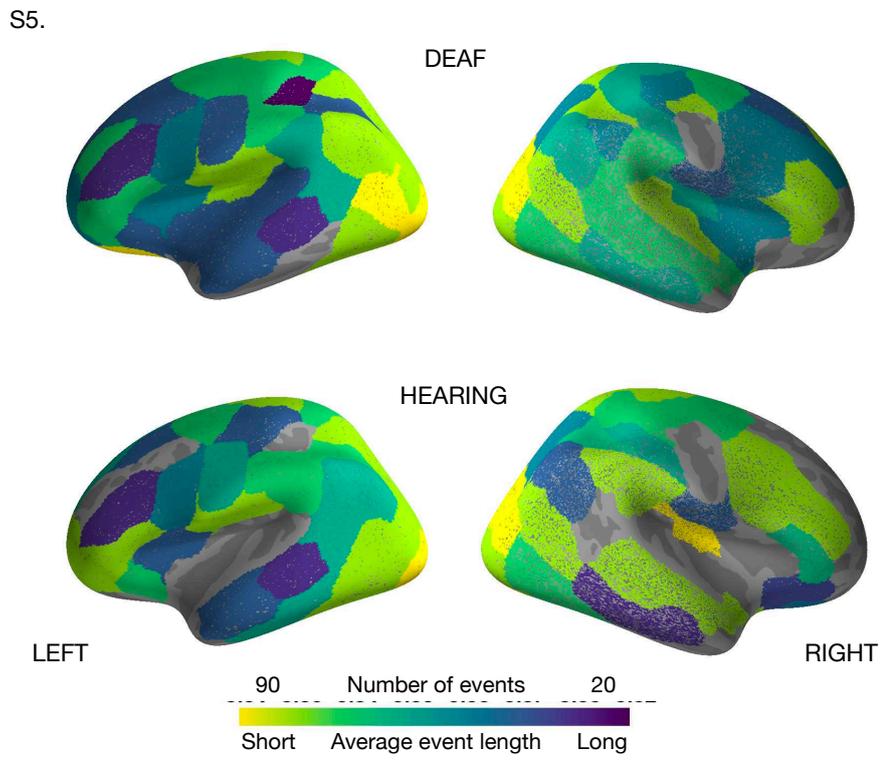


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S4. ROI analysis of temporal cortex. Bar plots demonstrate inter-subject correlation values (r) in the auditory cortex: (primary: Te1.0-Te1.2, secondary: Te2-Te3 and STS1) calculated for each condition and each group separately

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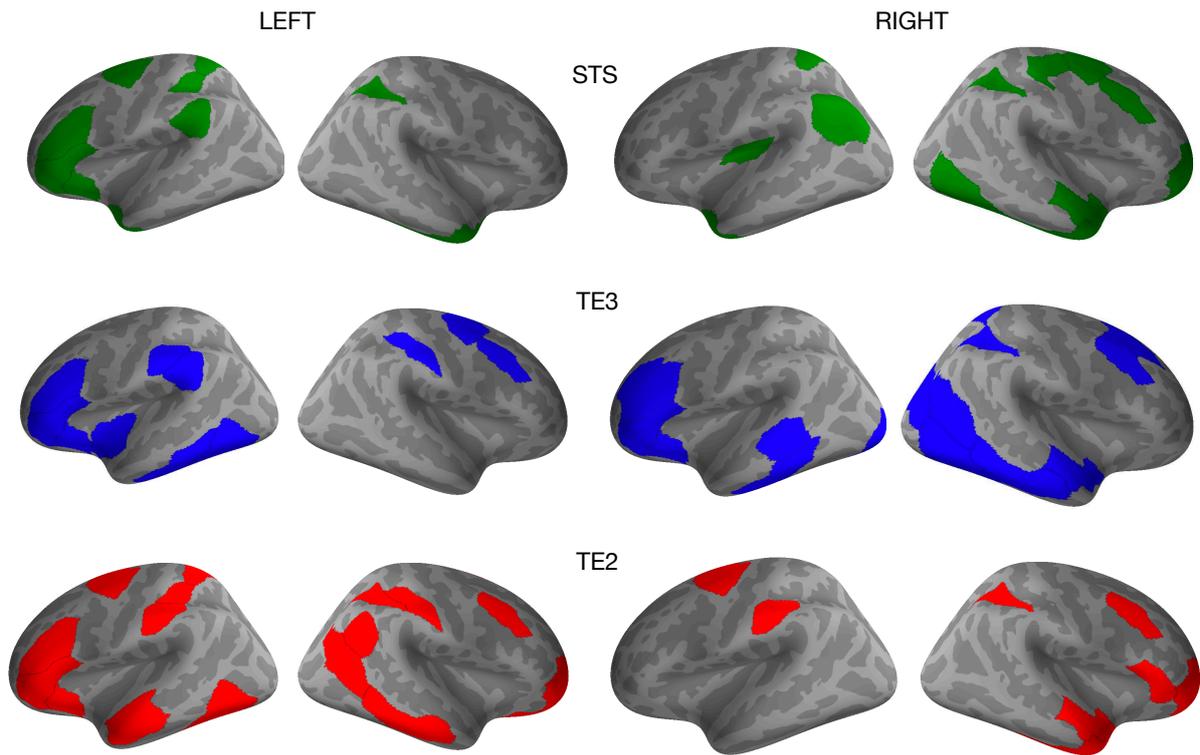
877 S5. Preferred number of events/ event length on the whole brain parcellation estimated using event

878 segmentation (Hidden Markov Models). Maps represent with significant models at the level <0.05

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S6.



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883 Fig. S6 Regions with significant match with the event structure recognised in the auditory ROIs (STS, Te3 and
884 Te2) The structure of the event boundaries was compared between ROIs of the temporal cortex and other brain
885 structures: all 100 parcels from Shaefer parcellation. We measured the match between these regions by
886 computing the fraction of boundaries in one ROI within three time points to boundaries in another ROI. The
887 three time points threshold was mean to adjust for an uncertainty in the model about exactly where an event
888 switch occurs. The significance of a match was calculated using permutation tests (number of permutations
889 across event bounds=1000) Maps represent only these parcels in which event structure match significantly event
890 structure in auditory ROIs ($p < 0.01$)

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