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Naturalistic auditory stories synchronize "visual" cortices across congenitally blind but not sighted individuals

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Title: Naturalistic auditory stories synchronize "visual" cortices across congenitally blind but not
 sighted individuals
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21 The authors declare no competing interests.

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30 Abstract

- 31 How does developmental experience, as opposed to intrinsic physiology, shape cortical
- 32 function? Naturalistic stimuli were used to elicit neural synchrony in individuals blind from birth
- (n=18) and those who grew up with sight (n=18). Blind and blindfolded sighted participants

34	passively listened to three audio-movie clips, an auditory narrative, a sentence shuffled version
35	of the narrative (maintaining language but lacking a plotline), and a version of the narrative
36	backwards (lacking both language and plot). For both groups, early auditory cortices were
37	synchronized to a similar degree across stimulus types, while higher-cognitive temporo-parietal
38	and prefrontal areas were more synchronized by meaningful, temporally extended stimuli (i.e.,
39	audio-movies and narrative). "Visual" cortices were more synchronized across blind than sighted
40	individuals, but only for audio-movies and narrative. In the blind group, "visual" cortex
41	synchrony was low for backwards speech and intermediate for sentence shuffle. Meaningful
42	auditory stimuli synchronize "visual" cortices of people born blind.

45 Significance

46	Naturalistic stimuli engage cognitive processing at many levels. Here, we harnessed this
47	richness to investigate the effect of experience on cortical function. We find that listening to
48	naturalistic audio-movies and narrative drives synchronized activity across "visual" cortices of
49	blind, more so than sighted, individuals. "Visual" cortex synchronization varies with
50	meaningfulness and cognitive complexity. Higher synchrony is observed for temporally
51	extended meaningful stimuli (e.g. movies/narrative), intermediate for shuffled sentences, lowest
52	for time varying complex noise. By contrast, auditory cortex was synchronized equally by
53	meaningful and meaningless stimuli. In congenitally blind individuals most of "visual" cortex is
54	engaged by meaningful naturalistic stimuli.

56 Introduction

57 Studies of blindness give insight into how intrinsic physiology and experience shape cortical function. Sensory loss early in life alters the response properties of sensory cortices. In 58 59 blindness, "visual" cortices are active during a variety of auditory and tactile tasks, including 60 motion detection, shape discrimination, sound localization, echolocation, Braille-reading and auditory sentence comprehension (Wanet-Defalque et al., 1988; Uhl et al., 1991; Sadato et al., 61 62 1996; Weeks et al., 2000; Bavelier and Neville, 2002; Röder et al., 2002; Merabet et al., 2004; 63 Gougoux et al., 2005; Poirier et al., 2006; Stilla et al., 2008; Collignon et al., 2011; Thaler et al., 2011; Wolbers et al., 2011). Transiently disrupting "visual" cortex activity with transcranial 64 65 magnetic stimulation (TMS) impairs verb-generation and Braille-reading performance (Cohen et al., 1997; Amedi et al., 2004). Questions remain about the nature and extent of this repurposing. 66 67 First, does variation in the localization of activation across studies stem from individual variability or is repurposing systematic and similar across blind individuals? Second, a given task 68 69 activates a small subset of "visual" cortices. What is the spatial extent of blindness-related 70 plasticity? Lastly, are repurposed cortices engaged during everyday behaviors? Experimental paradigms often use stimuli unlike those encountered in daily life. For example, "visual" cortices 71 72 respond to multi-clause sentences with syntactic movement, but such sentences are infrequent in 73 natural speech (Lane et al., 2015). Do deprived cortices come online only during such unusually 74 demanding cognitive tasks, i.e. as an "overflow" processor? 75 Insights into these questions come from an approach that is complementary to task-based

Insights into these questions come from an approach that is complementary to task-based
 studies, which uses naturalistic stimuli to drive brain activity during fMRI (Hasson et al., 2004).
 Movies and narrated stories are richly engaging – i.e., a cognitive "kitchen sink" where many
 processes are elicited. The data are analyzed by correlating activity of each cortical location

across participants. In this way, each participants' brain activity, serves as a model for others.
Such inter-subject correlation provides a natural measure of the degree to which the same
cortical location serves a similar function across individuals (Hasson et al., 2004; 2010 for
review).

83 The cortical synchronization approach can also provide insight into the types of cognitive 84 processes that colonize the occipital cortices in blindness. The type of stimuli that synchronize a 85 given cortical area relates to the types of cognitive functions the area supports (Hasson et al., 86 2004; 2008). In sighted subjects fronto-temporal semantic networks are synchronized by 87 cognitively complex naturalistic stimuli, such as movies and comedic skits. Disrupting the 88 cognitive content and temporal structure of these stimuli (e.g., by shuffling or presenting them backwards) dramatically reduces synchronization. In contrast, early auditory and visual cortices 89 90 synchronize comparably to meaningful and meaningless shuffled stimuli (Hasson et al., 2008; 91 Lerner et al., 2011; Naci et al., 2016). One interpretation of these results is that different cortical 92 areas have different temporal receptive windows: short temporal receptive windows for early 93 sensory areas and longer temporal receptive windows for higher-cognitive regions. Whether 94 temporal receptive windows are an intrinsic physiological property of cortical circuits or whether 95 they change in cases of functional reorganization is not known. In blindness, are the receptive 96 windows of the "visual" cortices short, like those of other sensory areas, or long, like those of 97 fronto-parietal networks? Is higher-cognitive content required to synchronize activity in "visual" 98 cortices of individuals who are blind from birth?

99 Congenitally blind and blindfolded sighted individuals listened to four intact naturalistic
100 stimuli (5 to 7 min each): three audio-movies and a spoken narrative called Pie-Man. Participants
101 also listened to a shuffled version of the narrative that preserved sentences but lacked a coherent

plotline and the narrative played backward, i.e., with no discernible semantic or linguistic
content (Lerner et al., 2011; Naci et al., 2014; 2016). Synchronization of activity in occipital
cortices was compared across blind and sighted participants, across stimulus types and with other
cortical areas.

106 Materials and Methods

107 Participants

108 18 congenitally blind (6 male; 13 right-handed, 2 ambidextrous; age: mean=41.87 SD=16.41; years of education: mean =16.72, SD=2.52) and 18 sighted controls (3 male; 16 right-109 110 handed; age: mean=41.23, SD=13.19; years of education: mean =18.39, SD=4.26) contributed 111 data to the current experiment (for further details, see Table S2 in Supplementary text on https://osf.io/r4tgb/). Blind and sighted participants were matched on average age and education 112 level (age: t(34)=0.13, p>0.5; education: t(34)=1.43, p=0.16). All blind participants self-reported 113 114 never having been able to distinguish colors, shapes, or motion. 11 of the 18 blind participants 115 had minimal light perception; the remainder had none. Participants had no known neurological 116 disorders, head injuries, or brain damage. For all blind participants, the causes of blindness excluded pathology posterior to the optic chiasm (see Table 1 for details). All participants gave 117 written consent under a protocol approved by the Institutional Review Board of Johns Hopkins 118 119 University. Five additional sighted and three additional blind individuals participated in the 120 experiment but were removed from analyses due to poor performance (see below). One 121 additional blind participant was removed from analyses because of subsequently reported temporary vision during childhood. Reported statistics refer only to participants included in 122 123 analyses.

124 Experimental design and statistical analyses

125

126 Stimuli and Procedure.

127 Participants listened to 4 intact and 2 scrambled entertainment clips while blindfolded 128 and undergoing functional magnetic resonance imaging (stimuli are posted to Open Science 129 Framework: https://osf.io/r4tgb/). Intact stimuli were excerpted from the audio tracks of movies 130 (Brian De Palma's Blow Out, Pierre Morel's Taken, and James Wan's The Conjuring) and a 131 spoken narration (Jim O'Grady's Pie-Man). To enable a shared interpretive experience across 132 participants, we chose intact clips to be suspenseful, entertaining, and easy to follow. Non-intact 133 stimuli were generated from the intact Pie-Man stimulus. The backward condition was timereversed to lack intelligible speech; sentence shuffle was spliced from intact, permuted sentences 134 135 to lack a coherent plotline. To construct the sentence shuffle stimulus, individual sentences were 136 clipped to make the shortest possible stand-alone sentence. Compound sentences were divided 137 into each of its standalone components, sometimes beginning with the word "and." This resulted 138 in 96 sentences (length: mean= 4.37 s, SD=3.43 s) that were randomly reordered such that newly adjoining sentences had an original distance of at least 4 sentences between them. Stimulus 139 140 features were as follows: backward/sentence shuffle/Pie-Man RMS amplitude=0.032, 141 frequency=1177; Blow Out RMS amplitude=0.054, frequency=4414; Taken RMS 142 amplitude=0.031, frequency=1600; The Conjuring RMS amplitude=0.110, frequency=2472 143 (sox.sourceforge.net). We also collected a rest run in which no stimulus was presented and participants were told to relax but not to fall asleep. 144 145 Before each auditory clip (and scan), participants were read a 2-3 sentence

146 contextualizing prologue to facilitate interpretation of the clip. After the entire scan-session,

147 participants were given an expected multiple-choice comprehension test for each intact clip. 148 There were five questions per clip and the questions probed detailed information, e.g. names of 149 characters, locations of events, and critical plot points. All stimulus data were excluded from 150 participants who did not correctly answer at least 3 out of 5 questions for at least 3 (out of 4) 151 intact runs. Additionally, for each intact clip, participant data were excluded if the participant 152 failed the comprehension assessment for that particular clip or if the participant reported having 153 previously seen the movie from which that particular clip was taken. Analyses thus included 15-154 18 participants per stimulus, per vision group. For each stimulus, blind and sighted participants 155 were statistically equivalent with respect to age and years of education. 156 Each auditory clip was preceded by 5 s of rest and followed by 20-22 s of rest. Stimuli were presented using Psychtoolbox (v 3.0.14) for Matlab; stimulus starts were triggered at the 157 acquisition of the first volume. We subsequently discarded the first 20 s and last 18 s of each 158 159 functional scan to remove scans with rest and the auditory stimulus onset (accounting for the 160 hemodynamic lag). The duration of each stimulus, not counting the rest periods before and after 161 the clip, were as follows: rest (7.4 min.), backward, sentence shuffle, and Pie-Man (6.8 min.), The Conjuring (5.1 min), Taken (5 min.), and Blow Out (6.5 min.). Presentation order of the six 162 stimuli were counterbalanced across participants, with blind and sighted participants yoked to 163 164 receive the same orderings. In addition to the comprehension questions, we also asked 3 165 questions to probe participants' subjective experience. Each participant rated each intact clip on suspense, entertainment, and following ease according to a 5-point Likert scale (for average 166 subjective ratings of clips, see Table S3 in supplementary text at https://osf.io/r4tgb/). 167 168 Auditory stimuli were presented over Sensimetrics MRI-compatible earphones

- 169 (http://www.sens.com/products/model-s14/) at the maximum comfortable volume for each
- 8

participant. To ensure that participants could hear the softer sounds in the auditory clips over the
scanner noise, a relatively soft sound (RMS amplitude=0.002, frequency=3479) was played to
participants during acquisition of the anatomical image; all participants indicated hearing the
sound via button press.

174

175 *MRI data acquisition and cortical surface analysis.*

176 MRI structural and functional data of the whole brain were collected on a 3 Tesla Philips 177 dStream Achieva scanner. T1-weighted structural images were collected in 150 axial slices with 178 1 mm isotropic voxels using a magnetization-prepared rapid gradient-echo (MP RAGE). T2*-179 weighted functional images were collected using a gradient echo planar imaging (EPI) sequence 180 (36 sequential ascending axial slices, repetition time (TR) 2 seconds, echo time (TE) 0.03 seconds, flip angle 70°, field of view (FOV), matrix 76 x 70, slice thickness 2.5 mm, inter-slice 181 182 gap 0.5, slice-coverage FH 107.5, voxel size 2.53 x 2.47 x 2.50 mm, PE direction L/R, first order 183 shimming). SENSE factor 2.0 was used as a parallel imaging method. The acquisition time and 184 number of volumes collected for each auditory clip were as follows: backward, shuffled, Pie-Man (7:42m, 223), Taken (5:54, 169), Blow Out (7:26, 215), The Conjuring (6:00, 172). Data 185 analyses were performed using FSL (v 5.0.9), Freesurfer (v 5.3), the HCP workbench (v 1.2.0), 186 187 and custom software (Dale et al., 1999; Smith et al., 2004; Glasser et al., 2013). 188 189 Preprocessing.

190 Functional data were motion corrected, slice-time corrected. Nuisance covariates (i.e.,

191 linear trend and any motion spikes-- timepoints with a root mean squared framewise-

displacement greater than 1.75 mm) were regressed out of the timeseries of all gray matter

voxels. As a result, motion spikes were set to the run-mean (number per run: sighted: 194 mean=0.23, SD=0.58; blind: mean=0.64, SD=0.88; t(34)=1.65, p=0.11). Resulting time-series 195 residuals were next high pass filtered with a 128 s cutoff. 196 Each participants' functional data were mapped to the surface after co-registering to their 197 own anatomical scan using FSL's FEAT. Next, each participant's anatomical scan was 198 normalized to a common surface-based template (fsaverage) using sulcal/gyral alignment (via 199 recon-all). Finally, functional data were projected to the surface, down-sampled to HCP's 32K 200 standard cortical surface, dilated and eroded by 2.5 mm to fill small holes. For whole-brain 201 analyses, data were smoothed with a 12 mm FWHM (on the surface) Gaussian kernel (Hagler et 202 al., 2006; Jo et al., 2007; Anticevic et al., 2008; Tucholka et al., 2012). Note that smoothing was 203 performed on the 2-dimensional surface, rather than in the 3-dimensional volume, a given 204 surface smoothing radius will encompass less surrounding tissue than the same smoothing radius 205 used in the volume. 12 mm of smoothing on the surface corresponds to approximately 8.5 mm 206 smoothing in the volume (Hagler et al., 2006). Timepoints before and after stimulus presentation 207 were trimmed (as noted above). Finally, so that participant timecourses would have comparable 208 intensity values, we scaled each timepoint by the grand-mean of the timeseries and then 209 multiplied each timepoint by 10,000.

210

193

211 Inter-Subject Whole-Cortex Correlation (ISC).

212 For each vertex in the cortex, we assessed the extent of stimulus-driven synchronization (i.e. correlation) to that same vertex in other people's cortices. Synchrony of brain activity was 213 214 determined within vision groups-- i.e., each congenitally blind individual's brain to the mean of 215 all other congenitally blind individuals and each sighted individual to the mean of all other

216	sighted individuals. For each run, we calculated vertex-wise synchrony as the average Pearson
217	product-moment correlation coefficient (r) between each subject's timecourse and the average of
218	the reference group (Hasson et al., 2004; Lerner et al., 2011). For example, the blind group's ISC
219	value at vertex 99 was calculated by correlating the timecourse of blind participant 1's vertex 99
220	to the mean timecourse in the blind group (without participant 1) of vertex 99, repeating for all
221	blind participants, and then averaging ISC values across blind participants. For both group
222	comparisons (i.e., blind to blind and sighted to sighted), averaged r-value ISC maps were
223	transformed to Fisher's z-values (i.e. arctanh(r)) to enable comparisons of correlations across
224	different stimuli/groups. Differences in synchronization between stimuli and/or between groups
225	were compared by subtracting the relevant z-maps (i.e. blind > sighted = blind - sighted). A
226	mean audio-movie synchronization map was created by averaging z-maps of the 3 intact audio-
227	movie stimuli-i.e., The Conjuring, Taken, Blow Out. Resulting z-maps were subsequently
228	back-transformed to r-maps (i.e. tanh(r)).
229	Because ISC maps violate several assumptions of parametric hypothesis testing, we
230	performed a non-parametric, permutation analysis to assess the statistical significance of the
231	inter-subject correlations (Lerner et al., 2011; Regev et al., 2013). We generated a null
232	distribution by permuting the original data. Each preprocessed timecourse was first Fourier
233	transformed to obtain absolute values and phases of each timecourse frequency. Timecourses
234	were permuted by re-ordering the phases of the empirical timecourses and then applying an
235	inverse Fourier transform on these permuted phases and to the original amplitudes (Lerner et al.,
236	2011; Regev et al., 2013). Phase randomization was independent across participants but the same
237	for all vertices within a participant. This procedure maintained autocorrelation and spatial non-

- 238 independence across cortex, which is observed in empirical timecourses. ISC values, for all
- 11

stimuli and comparisons, were calculated on these permuted "null" timecourses, in the same way
as the non-permuted real data analysis. A null distribution, for each stimulus and comparison,
was obtained by repeating the procedure 1000 times.

242 We implemented a "vertex-wise" correction for multiple comparisons to control for the 243 familywise error (FWE) rate of the multiple comparisons across the cortex. Only the largest ISC 244 value across all brain cortices, in each of the 1000 permutations, contributed to the null 245 distribution. We rejected the null hypothesis for a particular comparison if the real data's ISC 246 value was in the upper 5% of all 1,000 values in each null distribution (Simony et al., 2016; 247 Nichols et al., 2001). The statistical test is, therefore, one tailed. The resulting Pearson 248 correlation thresholds for contrasts examined varied from 0.10 - 0.25. Differences in criteria reflect different variances for each of the null sampling distributions, likely due to differences in 249 250 degrees of freedom amongst the stimuli (e.g., number of timepoints) and between numbers of 251 participants in each contrast, as well as the computation performed (e.g. the audio-movies > 252 backward" comparison subtracts movie ISC values from backward ISC values and, therefore, 253 sums the variances of both the audio-movies and backward distributions). Since the sighted group's ISC criteria were a bit higher than the blind group's ISC criteria, we thresholded sighted 254 255 ISC Figure 1 with the blind group's criteria to more conservatively test our hypothesis that the 256 sighted group's visual cortices will not synchronize for the non-visual stimuli. Results were 257 qualitatively the same as those obtained by using the sighted group's own criteria. 258 The vertex-wise correction for multiple comparisons described above is highly conservative, as there is a 5% probability of rejecting one or more true nulls in each 64,000 259

vertex family of statistical tests. Therefore, we used a "cluster-wise" correction (p < 0.05) to

261 control for the familywise error (FWE) rate of the multiple comparisons across the cortex for

262	contrasts between groups (i.e., blind ISC > sighted ISC for the backward stimulus) and for
263	contrasts between conditions that differ only subtly (i.e. Pie-Man > sentence shuffle) (Eklund et
264	al., 2016; Kessler et al., 2017). Rather than form a null-distribution from the highest vertex-wise
265	ISC values in each permutation across the whole cortex, we first generated an uncorrected alpha
266	criterion (of $p < 0.001$) by taking the r-value higher than 99.9% of all permutations (for each
267	vertex) and averaging this value across all vertices. Next, phase-randomized ISC maps were
268	thresholded at this criterion and assessed for maximum cluster size. For each of the 1000
269	permutations, a maximum whole-cortex cluster was obtained (for each stimulus and
270	comparison). The size of the maximum ISC clusters thus form a null distribution of cluster size.
271	Cluster-correction criteria at $p < 0.05$ were, likewise, set as the cluster-size larger than 95% of all
272	other clusters. Real-data ISC maps were cluster-corrected by first thresholding each vertex at the
273	uncorrected $p < 0.001$ criterion and then thresholding clusters at the cluster-wise threshold of $p < 0.001$
274	0.05. Cluster criteria for reported contrasts ranged from 45 - 88 mm.
275	

276 Inter-subject correlation (ISC) ROI analysis.

277 We defined three bilateral ROIs: V1, A1 and higher-cognitive posterior lateral temporal 278 (PLT) cortex. We used a primary visual cortex (V1) ROI from a previously published anatomical 279 surface-based atlas (PALS-B12; Van Essen, 2005). We defined an early auditory cortex ROI as 280 the transverse temporal portion of a gyral based atlas (Morosan et al., 2001; Desikan et al., 281 2006). For brevity, the early auditory cortex ROI will be abbreviated to A1, although it may not 282 be strictly limited to primary auditory cortex. A higher-cognitive bilateral posterior lateral 283 temporal (PLT) ROI was taken from parcels that responds to high-level linguistic content in 284 sighted subjects. The ROI was originally defined in the left hemisphere as responding more to

sentences than lists of nonwords in a large sample of sighted participants (Fedorenko et al.,
2010). This portion of lateral temporal cortex has shown sensitivity to a wide range of high-level
linguistic information, including word and sentence level meaning to sentence structure
(Bookheimer, 2002). The ROI was mirrored to the right hemisphere to match it with the bilateral
V1 and A1 ROI and since right hemisphere areas have been shown to respond to high-level
aspects of language such as discourse, context and metaphor, that are present in naturalistic
stimuli (Vigneau et al., 2011).

ROI analyses were performed on unsmoothed functional data. For each participant, a timecourse was obtained for each ROI by averaging across all vertices present in the bilateral ROI. From here, ISC analysis proceeded as in the whole brain analysis. For each ROI, each participant's ROI timecourse was correlated to the average ROI timecourse of all participants in the leave-one-out group (for within vision group analysis) or to the whole group (for across vision group analysis).

All statistics for factor comparisons (i.e. ROI, group, and/or conditions) were obtained by subtraction of the relevant z-transformed-r ISC values. For example, within A1 sighted group: backward ISC vs. rest ISC = A1 sighted backward z-transformed-r ISC - A1 sighted rest z-

transformed-r ISC. Fisher's z-transformed-r ISC values were subsequently transformed back to r
 (correlation coefficient) values for reporting.

303 Statistical significance of ROIs was assessed as in the whole-brain analysis. Timecourse 304 data were permuted 1,000 times as described above to generate a null distribution. Critically, for 305 ROI analysis, we permuted the ROI timecourse after aggregating across vertices. This generates 306 a realistic timecourse signal that accounts for the lack of independence amongst spatially 307 proximal vertices. Using these null ROI timecourses, analysis proceeded as in the empirical ROI

308	ISC analysis. As in the empirical ROI analysis, statistics for all factor comparisons were
309	generated by subtracting the relevant ISC-ROI values from the permuted timecourse. Doing so
310	over all permutations resulted in a null distribution for each statistic. Reported probabilities were
311	calculated relative to that statistic's null distribution (formed by performing the relevant
312	subtractions over null distribution values for each component). Probabilities reflect the
313	proportion of null values whose magnitude is greater than, or equal to, the empirically observed
314	value. ROI tests for statistical significance are thus two-tailed. Empirical values are considered
315	significantly different from the null hypothesis if $p < 0.05$.

317 Results

318 *High inter-subject correlation in the "visual" cortices of blind individuals for audio-movies and*319 *narrative: whole-cortex analysis*

320 We used whole-cortex inter-subject correlation analysis to compare synchrony across 321 blind and sighted groups, and across intact and shuffled stimuli. Within the blind, but not the 322 sighted group, there was significant inter-subject synchronization in the occipital cortices for the audio-movie stimuli, bilaterally on medial, lateral, and ventral occipital cortices and absent only 323 on the posterior occipital cortices (Figure 1; p < 0.05, corrected). By contrast, the backwards 324 325 stimulus did not significantly drive synchronization within the occipital cortices of blind 326 individuals (Figure 1; p < 0.05, corrected). A direct comparison revealed higher inter-subject 327 synchronization for audio-movies than for the backward stimulus within the primary "visual" cortices of the blind group (Figure 1; p < 0.05, corrected). Overall, 65.04% of occipital cortices 328 329 (occipital lobe parcel from PALS-B12 atlas; Van Essen, 2005) were significantly synchronized 330 across blind participants during audio-movie listening. Across each of the four intact stimuli,

333 A direct comparison of vision groups revealed that the audio-movie stimuli drove higher 334 synchronization in the blind group, than in the sighted group, extensively across the occipital 335 cortices (Figure 1; p < 0.05, corrected). An interaction contrast (blind > sighted x audio-movies > 336 backward) revealed areas along the lateral, medial, and ventral occipital cortices in which a 337 greater increase in synchronization for audio-movies, compared to the backward stimulus, was 338 observed within the blind group than within the sighted group (Figure 1; p < 0.05, corrected). 339 Relative to meaningful naturalistic stimuli, auditory backward also produced less 340 synchrony in higher cognitive lateral temporal, precuneus and prefrontal areas among both 341 sighted and blind groups. For the backwards stimulus, significant inter-subject synchronizations were observed only in the transverse temporal gyrus (Figure 1; p < 0.05, corrected). By contrast, 342 343 intelligible auditory movies, as well as Pie-Man, evoked significant additional inter-subject 344 synchronization across the superior and middle temporal gyri/sulci, angular gyrus, precuneus, 345 inferior frontal gyrus/sulcus, and the middle frontal junction (Figure 1; p < 0.05, corrected). For 346 both blind and sighted groups, a direct comparison of the audio-movies and backward stimuli 347 revealed significantly more synchronization for audio-movies along the superior/middle 348 temporal gyri/sulci and precuneus (Figure 1; p < 0.05, corrected). Similar but weaker results 349 were obtained for Pie-man compared to backwards (Figure 3; p < 0.05, corrected). The sentence 350 shuffle condition produced an intermediate pattern between audio-movies/Pie-man and backwards speech (Figure 3; p < 0.05, corrected). 351

For completeness, we also correlated brain activity between blind and sighted groups
directly. Non-occipital cortices were synchronized similarly across groups as they were within

groups (Figure 4; p < 0.05, corrected). Additionally, we observed synchronization across vision
groups bilaterally along the calcarine sulcus. Overall, audio-movies appear to synchronize
occipital cortices across groups more than backward speech. However, the degree of synchrony
in V1 was lower across vision groups than within the blind group.

358

Effects of stimulus meaningfulness on correlations in V1, A1 and language-responsive posterior
lateral temporal (PLT) cortex: ROI analysis

We conducted a region of interest analysis to more closely examine the inter-subject synchronization profiles of three regions of interest – the primary visual cortex (V1), the early auditory cortex (A1), and a higher-cognitive area that is involved in language processing (PLT) – across stimulus types and vision groups. Results are displayed in Figure 5. Because of the large number of possible comparisons (between 15 and 21 per group and region), we describe the observed pattern and test only those comparisons that are most critical.

367 In early auditory cortex of both groups, all stimuli drove high inter-subject

368 synchronization. Two audio-movies, Taken and Conjuring, produced greater synchrony in A1

369 relative to the third audio-movie (Blow Out) as well as relative to all of the other audio stimuli

370 (Figure 5; sighted A1: Taken vs. Blow Out, r=0.24, p<0.001, Conjuring vs. Blow Out, r=0.37,

371 p<0.001; blind A1: Taken vs. Blow Out, r=0.23, p<0.001, Conjuring vs. Blow Out, r=0.24,

p<0.001), possibly due to low-level differences between these movies and the other stimuli.

373 These two movies also produced higher levels of synchrony in PLT (Figure 5; sighted PLT:

Taken vs. Blow Out, r=0.13, p=0.026, Conjuring vs. Blow Out, r=0.13, p=0.018; blind PLT:

375 Taken vs. Blow Out, r=0.21, p<0.001, Conjuring vs. Blow Out, r=0.14, p=0.009).

376 Overall, Pie-Man produced similar levels of synchrony to backwards speech and sentence

377	shuffle in A1, with the exception of slightly higher synchrony for Pie-Man than Sentence Shuffle
378	(but not than backwards speech) in the sighted group (Figure 5; sighted A1: Pie-Man vs.
379	Backward, r=0.05, p =0.2, Pie-Man vs. Sentence Shuffle, r = 0.09, p=0.018; blind A1: Pie-Man
380	vs. Backward, r=0.04, p=0.308, Pie-Man vs. Sentence Shuffle, r = 0.04, p=0.333). In PLT, Pie-
381	Man and sentence-shuffle produced higher levels of synchrony than backwards speech (Figure 5;
382	sighted PLT: Pie-Man vs. Backward r=0.14, p<0.001, Sentence Shuffle vs. Backward, r=0.16,
383	p<0.001; blind PLT: Pie-Man vs. Backward r=0.09, p=0.043, Sentence Shuffle vs. Backward,
384	r=0.09, p=0.048). Note that the sentence shuffle and backwards speech stimuli were created from
385	the Pie-Man stimulus and are thus matched to it (but not to the audio movies) on low-level
386	auditory features, such as frequency and amplitude variation. Crucially, synchrony in V1 varied
387	as a function of group and condition. The sighted showed low-levels of synchrony across all
388	auditory stimuli in V1, although, one of the audio-movies that produced higher synchrony in
389	both A1 and PLT (Conjuring) also produced some synchrony in V1 of the sighted group (Figure
390	5; sighted V1: Backward vs. Rest, r=0.01, p>0.5, Sentence Shuffle vs. Rest, r=0.06, p=0.197,
391	Pie-Man vs. Rest, r=-0.09, p=0.064, Blow Out vs. Rest, r=0.05, p=0.296, Taken vs. Rest, r=0.01,
392	p>0.5, Conjuring vs. Rest, $r = 0.10$, $p=0.046$). In the blind group, all three movies as well as Pie-
393	Man and to a lesser degree sentence shuffle produced high synchrony (Figure 5; blind V1:
394	Sentence Shuffle vs. Rest, r=0.10, p=0.036, Pie-Man vs. Rest, r=0.19, p<0.001, Blow Out vs.
395	Rest, r=0.21, p<0.001, Taken vs. Rest, r=0.29, p<0.001, Conjuring vs. Rest, r = 0.29, p<0.001).
396	No synchrony was observed for backward speech (Figure 5; blind V1: Backward vs. Rest,
397	r=0.02, p>0.5). V1 of the blind group demonstrated significantly higher synchronization than V1
398	of the sighted group, but only for the intact stimuli (Figure 5; V1 blind vs. sighted: backward, r =
399	0.003, p>0.5, Sentence Shuffle r=0.125, p=0.004, Pie-Man, r = 0.24, p<0.001; Blow Out, r=0.18,

p=0.001, Taken, r= 0.26, p<0.001, Conjuring, r=0.26, p<0.001). The blind, but not the sighted,
group showed a significant difference between Pie-Man and backwards speech (Figure 5; V1:
group (blind vs. sighted) x condition (Pie-Man vs. backward) interaction r=0.24, p<0.001).

403

404 Sighted to Blind ROI Inter-Subject Correlations

405 As in the whole brain analysis, we assessed common functionality across vision groups 406 by directly correlating sighted individuals to the blind groups, and vice-versa. We found similar

407 levels of synchrony in A1 and PLT across, as within, groups (Figure 5; across group A1:

408 backward vs. rest, r=0.36, p<0.001; sentence shuffle vs. rest, r=0.36, p<0.001; Pie-Man vs. rest,

409 r=0.35, p<0.001, audio-movies vs. rest, r=0.47, p<0.001; PLT: backward vs. rest, r=0.07, p=0.02;

410 sentence-shuffle vs. rest, r=0.19, p<0.001; Pie-Man vs. rest, r=0.20, p<0.001, audio-movies vs.

- 411 rest, r=0.41, p<0.001; A1 audio-movies: across group vs blind group, r =0.03, p=0.19; across
- 412 group vs. sighted group: r=0.04, p=0.13; PLT audio-movies: across group vs blind group, r

413 =0.004, p>0.5; across group vs. sighted group: r=0.002, p>0.5).

In V1 we observed low but significant levels of correlation between the blind and sighted 414 415 subjects for the 3 movies, but not for the other intact stimulus, Pie-Man (Figure 5; across group V1: backward vs. rest, r = 0.04, p = 0.27; sentence-shuffle vs. rest, r = 0.06, p = 0.07; Pie-Man 416 417 vs. rest, r = 0.03, p = 0.4, movies > rest, r = 0.17, p < 0.001). Overall, synchrony in V1 for the 418 movie stimuli was lower across vision groups than within the blind group (across group vs blind group: audio-movies, r = 0.16, p < 0.001) and higher than within the sighted group (across group 419 420 vs sighted group: audio-movies, r = 0.06, p = 0.03). Also, unlike V1 synchronization within the 421 blind group, V1 synchronization across vision groups did not systematically increase with

422 increasing cognitive complexity of the stimuli (Figure 5; across group V1: Pie-Man + Blow Out

vs. backward, r=0.05, p=0.10). The effect of cognitive complexity on V1 synchronization was
significantly smaller in the across group correlation than in the blind group and no different from
that within the sighted group (Figure 5; V1: group (blind vs. across group) x condition (Pie-Man
+ Blow Out vs. backward) interaction r=0.17, p=0.001; group (sighted vs. across group) x
condition (Pie-Man + Blow Out vs. backward) interaction r=0.07, p=0.2).

428

429 Discussion

"Visual" cortices of blind individuals synchronize to each other during naturalistic 430 431 listening to auditory movies and a narrative. The audio-track of movies drove collective 432 responding in 65% of the "visual" cortices, by surface area. Synchronization was observed 433 bilaterally, and spanned both retinotopic and higher order areas on the lateral, medial, and ventral 434 surfaces of the occipital lobe. This is a lower, rather than an upper, bound to the topographical 435 extent of "visual" cortex repurposing, since failure to synchronize could occur because the 436 particular naturalistic stimuli used in the current study did not contain relevant cognitive content 437 for some subset of "visual" cortices. The current findings are consistent with the idea that, in 438 blindness, most of the available cortical tissue undergoes systematic adaptation for everyday 439 tasks.

A key observation is that meaningful temporally extended naturalistic stimuli (i.e.,
auditory movies and narratives) synchronize "visual" cortices of blind individuals more than
stimuli that are meaningless. "Visual" cortices of blind individuals showed little synchrony while
listening to a nonsense backward auditory stream. This finding is consistent with a recent
magnetoencephalography (MEG) study that observed greater synchrony for intelligible than
unintelligible speech in foveal V1 of the blind participants (van Akeren et al., 2018). We found

that the shuffled sentences condition, which contains some meaning but no plot, synchronized
"visual" cortices of the blind group (and fronto-temporal cortices of both groups) to an
intermediate degree. In sum, "visual" cortices of blind individuals synchronize to a shared
experience of meaningful naturalistic stimuli.

450 Previous work has used the observations of varying levels of synchrony across stimuli of 451 different cognitive complexity to characterize the "temporal response window" of different 452 cortical networks (Hasson et al., 2008; Lerner et al., 2011). According to this framework, cortical 453 networks differ according to the length of the temporal window over which they integrate 454 information. Higher cognitive areas integrate information over longer time windows and 455 therefore synchronize only for stimuli that have structure at this long timescale. By contrast, lowlevel sensory areas, including early auditory cortices and early visual cortices of sighted 456 457 individuals, integrate information only over short time windows. As a result, stimulus structure at 458 longer time scales has no effect on the levels of synchrony in these early sensory areas (Hasson 459 et al., 2008). Here we find that in blind individuals "visual" cortices exhibit a long temporal 460 response window that is comparable to that of higher-order cognitive areas, such as the posterior 461 lateral temporal cortex. These results suggest that the temporal response window of a cortical 462 area is not intrinsic to its anatomy at birth. 463 The present results are consistent with and complementary to evidence from studies using

task-based designs. Previous studies suggest that deafferented visual cortices are engaged in a
wide range of auditory and tactile experimental tasks, including motion detection, shape
discrimination, sound localization, echolocation, Braille-reading and auditory sentence
comprehension (Wanet-Defalque et al., 1988; Uhl et al., 1991; Sadato et al., 1996; Weeks et al.,
2000; Bavelier and Neville, 2002; Röder et al., 2002; Merabet et al., 2004; Gougoux et al., 2005;

469	Poirier et al., 2006; Stilla et al., 2008; Collignon et al., 2011; Thaler et al., 2011; Wolbers et al.,
470	2011). Particularly relevant, "visual" cortices of blind individuals are active during memory
471	recall (e.g. when naming words from a previously memorized list) and are sensitive to linguistic
472	meaning and structure (Amedi et al., 2003; Raz et al., 2005; Bedny et al., 2011; Lane et al.,
473	2015; Röder et al., 2002). For example, the "visual" cortices of blind individuals respond more to
474	sentences than to lists of unrelated words and more to grammatically complex than
475	grammatically simple sentences (Röder et al., 2002; Bedny et al., 2011; Lane et al., 2015).
476	Naturalistic stimuli of the type used in the current study likely engaged some of these and
477	additional diverse cognitive processes. Processing audio-movies and narratives involves
478	language comprehension, recall of past information, selective attention, integrating across
479	relevant plot points and predicting upcoming events during movie watching (Naci et al., 2014).
480	Synchrony of "visual" cortex activity across individuals suggests that such processes do not
481	idiosyncratically colonize different parts of visual cortex in different blind individuals and are
482	not only engaged in artificial task conditions.
483	The present results leave open several important questions. The complex naturalistic
484	stimuli used in the current study synchronized large swaths of deafferented "visual" cortex,
485	including not only V1 but also extending into lateral and ventral occipito-temporal areas.
486	Previous research suggests that "visual" cortex is not colonized for a single non-specific process
487	in blindness. Rather "visual" cortices participate in an array of distinct cognitive operations and
488	naturalistic stimuli engage many of these processes at once (e.g. Kanjlia et al., 2016; Abboud &
489	Cohen, 2019). Further work is needed to delineate whether different portions of this
490	synchronized network support different cognitive functions and if so to identify the nature of
491	these functions.

A further open question concerns the way in which intrinsic physiology shapes the function of "visual" cortex and precisely what is shared and what is different in the function of this cortical system across sighted and blind people. A key finding of the current study is greater synchrony of 'visual' cortices across blind as compared to sighted adults. However, even in the sighted (blindfolded) group we observed some synchrony of 'visual' cortices. In particular, the same audio-movie stimulus produced the highest synchrony across all tested brain regions and across both groups.

499 While providing evidence for functional plasticity, the present results also illustrate ways 500 in which innate constraints shape cortical function even in blindness. First, synchronization of 501 "visual" cortices across blind individuals suggests the presence of systematically localized 502 cortical function across individuals even in cases of atypical sensory experience. Such 503 systematicity is likely related to common anatomical constraints. Future work using techniques 504 such as hyper-alignment (Haxby et al., 2011) could provide insight into whether functional 505 specialization of cortex is more variable across individuals in cases where the cortical region is 506 receiving species-atypical information from the environment.

507 Secondly, although synchrony of visual cortices was much lower across sighted than 508 blind individuals, even among the sighted, two of the three movies produced some 509 synchronization. Furthermore, when blind and sighted data were directly correlated with each 510 other, we observed some synchrony between foveal V1 of the sighted group and V1 of the blind 511 group. Again, the degree of this synchrony was low, relative to what was observed among individuals who are blind and unlike in the blind group, synchronization did not vary 512 513 systematically across stimulus meaningfulness. The existence of some synchrony even in the 514 sighted nevertheless suggests that non-visual information is reaching "visual" cortices in this

515	population. Further support comes from evidence that "visual" cortices are active in sighted
516	individuals during some non-visual tasks although, although the tasks and stimuli that elicit these
517	responses are different from those reported in studies of blindness (Sathian et al., 1997;
518	Zangaladze et al., 1999; James et al., 2002; Facchini and Aglioti, 2003; Merabet et al., 2004;
519	Sathian, 2005; Merabet et al., 2008; Voss et al., 2016). Thus, exactly how the function of
520	"visual" cortex is changing in blindness remains to be fully understood. There may be different
521	types and degrees of functional change across different anatomical locations within the visual
522	system. Some occipito-temporal areas previously believed to perform modality-specific visual
523	functions (e.g. scene perception) show preferential responses to analogous stimuli (e.g. names or
524	sounds characteristic of places) in blind participants (e.g. He et al., 2013; Peelen et al., 2003;
525	Striem-Amit and Amedi, 2014; van den Hurk et al., 2017). Conversely, large swaths of early
526	"visual" cortices respond to abstract cognitive functions, including grammar, in people who are
527	blind more so than those who are sighted (Bedny et al., 2011; Lane et al., 2015). Precisely in
528	which ways the functions of these regions are similar and different across blind and sighted
529	populations in each of these cases remains to be fully understood.
530	The available evidence suggests that innately determined long-range connectivity
531	patterns guide functional specialization by constraining the types of input that a cortical area

- 532 receives (O'Leary, 1989; Johnson, 2000; Dehaene and Cohen, 2007; Mahon and Caramazza,
- 533 2011; Saygin et al., 2016; Bedny, 2017; Cusack et al., 2018). Blindness, nevertheless, modifies
- 534 what "visual" cortex does with incoming, non-visual information suggesting that intrinsic
- 535 cortical anatomy allows for different functionals profiles depending on experience.

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Figures.



701 Figure 1. Whole-Cortex Inter-Subject Correlations

- 702 Inter-subject correlations (ISC) for the backward stimulus, all audio-movie stimuli, and for the
- 703 comparison of audio-movie greater than backward (MV > BW). Synchronization is shown
- 704 within the sighted group and within the blind group, vertex-wise corrected for multiple
- comparison at p < .05. A comparison of blind group synchronization greater than sighted group
- synchronization (Blind > Sighted) is also shown, vertex-wise thresholded at p < 0.001
- uncorrected and cluster-corrected for multiple comparison at p < 0.05.



- 10 Figure 2. All Stimuli, Sighted and Blind Inter-Subject Correlations
- 711 Inter-subject correlations (ISC) for each stimulus within the sighted and within the blind group,
- 712 vertex-wise corrected for multiple comparison p < .05.



715 Figure 3. Inter-Subject Correlation Comparisons

716 Comparisons of inter-subject correlations (ISC) for sentence shuffle > backward, Pie-Man >

517 sentence shuffle, and Pie-Man > backward. Synchronization is shown within the sighted group

and within the blind group. A comparison of blind group synchronization greater than sighted

719 group synchronization (Blind > Sighted) is also shown. All images are vertex-wise thresholded

720 at p < 0.001 uncorrected and cluster-corrected for multiple comparison at p < 0.05.



- 721
 722
 723 Figure 4. Inter-subject correlations between vision groups
- 724 Inter-subject correlations between vision groups (i.e. sighted to blind and blind to sighted),
- shown for the backward stimulus, the movie stimuli, and for movie > backward (i.e. MV > BW).
- 726 All figures are vertex-wise corrected for multiple comparisons.





Figure 5. Inter-subject correlations within regions of interest (ROI)

733 Inter-subject correlations (ISCs) of the sighted group, blind group, and across vision groups.

734 ISCs are shown for select conditions within early auditory cortices (A1), primary visual cortices

735 (V1), and the posterior lateral temporal (PLT) cortex. ROIs are displayed in the left hemisphere,

but inter-subject correlations are assessed bilaterally. Movies appear in the order listed.

737 Tables

738

Blindness Etiology	Ν
Leber Congenital Amaurosis	7
Retinopathy of Prematurity	5
Optic Nerve Hypoplasia	3
Retinitis Pigmentosa	1
Unknown	2

739

740 Table 1.

741 Total N(umber) of participants for each cause of blindness.