

Naturalistic Audio-Movies reveal common spatial organization across “visual” cortices of different blind individuals

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Abstract

Occipital cortices of different sighted people contain analogous maps of visual information (e.g. foveal vs. peripheral). In congenital blindness, “visual” cortices respond to nonvisual stimuli. Do visual cortices of different blind people represent common informational maps? We leverage naturalistic stimuli and inter-subject pattern similarity analysis to address this question. Blindfolded sighted ($n=22$) and congenitally blind ($n=22$) participants listened to 6 sound clips (5–7 min each): 3 auditory excerpts from movies; a naturalistic spoken narrative; and matched degraded auditory stimuli (Backwards Speech, scrambled sentences), during functional magnetic resonance imaging scanning. We compared the spatial activity patterns evoked by each unique 10-s segment of the different auditory excerpts across blind and sighted people. Segments of meaningful naturalistic stimuli produced distinctive activity patterns in frontotemporal networks that were shared across blind and across sighted individuals. In the blind group only, segment-specific, cross-subject patterns emerged in visual cortex, but only for meaningful naturalistic stimuli and not Backwards Speech. Spatial patterns of activity within visual cortices are sensitive to time-varying information in meaningful naturalistic auditory stimuli in a broadly similar manner across blind individuals.

Key words: blindness; naturalistic stimuli; plasticity; synchrony; visual cortex.

Introduction

Cognitive and perceptual processes localize to similar anatomical areas across people, as observed in retinotopic maps in V1 (e.g. [Serenio et al. 1995](#); [DeYoe et al. 1996](#); [Engel et al. 1997](#)). How do innate constraints and experience interact to produce these common informational maps? One way to gain insight into this question is to compare cortical organization across populations with different developmental experiences: people with and without vision.

Previous research finds that blindness enhances “visual” cortex responses during auditory, tactile, and higher cognitive tasks, such as Braille reading, sound localization, and spoken language comprehension ([Sadato et al. 1996](#); [Röder et al. 2002](#); [Bedny et al. 2011](#); [Collignon et al. 2011](#); [Kanjlia et al. 2016](#)). Do visual cortices of people born blind develop similar representational maps across individuals? Alternatively, do such common maps only emerge when visual cortices assume their evolutionarily predisposed visual functions?

Most neuroimaging studies of visual cortex plasticity in blindness have targeted a single cognitive process (e.g. sound localization, language) using simplified experimental designs (e.g. [Poirier et al. 2006](#); [Thaler et al. 2011](#)).

A handful of studies have identified anatomically separable responses to 2 or 3 information types within “visual” cortices of blind people (e.g. language vs. math) ([Kanjlia et al. 2016](#); [Abboud et al. 2019](#)). Recent studies find that the ventral occipito-temporal (OT) and early visual cortices of people born blind show spatially distinct responses to stimuli from different semantic categories (e.g. faces and places) when these are presented either via touch or auditorily ([Pietrini et al. 2004](#); [van den Hurk et al. 2017](#); [Mattioni et al. 2020](#); [Ratan Murty et al. 2020](#); [Vetter et al. 2020](#)). How consistent are such information “maps” across blind individuals? We test this question by directly comparing cortical maps across blind and sighted people using naturalistic auditory stimuli (i.e., audio clips from movies, narrative) using shared pattern analysis.

Naturalistic sounds, such as movie excerpts and spoken narratives, contain a range of rich information, from low-level perceptual to higher order semantic features. Such stimuli elicit synchronized activity across the brains of different people in both higher cognitive (e.g. frontotemporal) and sensory (e.g. auditory) networks ([Lerner et al. 2011](#)). Two recent studies presented blind participants with naturalistic auditory stimuli and reported that, unlike low-level control stimuli

(Backwards Speech), meaningful stimuli elicit synchronous activity in “visual” cortices of different congenitally blind (CB) individuals, mirroring the synchrony patterns observed in frontotemporal networks of sighted and blind people (Van Ackeren et al. 2018; Loiotile et al. 2019).

Recently developed shared-pattern functional magnetic resonance imaging (fMRI) analysis techniques find that meaningful naturalistic stimuli induce not only synchronized univariate activity but also shared “time-varying spatial patterns” of activity in higher-order semantic networks (Chen et al. 2017; Zadbood et al. 2017; Baldassano et al. 2018). Each segment (~10 s) of an unfolding narrative induces a characteristic spatial pattern of activity that is similar across people and distinct from other segments in the narrative (Chen et al. 2017; Zadbood et al. 2017; Baldassano et al. 2018). Here we leverage this approach to quantify and compare information maps across visual cortices of different blind individuals.

CB and sighted blindfolded adults listened to auditory excerpts from popular live action movies and a spoken narrative (5–7 min) while undergoing fMRI. Participants also heard 2 control stimuli: one in which the narrative sentences were shuffled to disrupt the plotline, and the narrative played in reverse (Backwards Speech), removing semantic and linguistic information. We measured spatial activity patterns evoked by each 10-s segment of the meaningful (movies and narrative) and control (shuffled sentences and Backwards Speech) stimuli and used inter-subject spatial correlation analyses to test for shared, segment-specific patterns among individuals within each group. We predicted that the meaningful stimuli, but not controls, would reveal consistent information maps across blind people in visual cortex.

Materials and methods

Participants

Twenty-two CB (8 males) and 22 sighted (S, 4 males) individuals contributed data to this study. All blind participants reported having minimal or no light perception since birth, such that they could not perceive motion, colors, or shapes. Sighted participants reported normal or corrected-to-normal vision. The sample size was determined by previous sample sizes and participant availability. We first scanned all of the CB participants that could be recruited within an approximately 3-month period. We then scanned an equal number of sighted control participants. In prior studies, we have observed group differences in neural responses to auditory stimuli with similar sample sizes to those reported here. Groups were matched on average age (CB mean = 43.5, SD = 16.9; S mean = 42.7, SD = 13.8, $t(21) = -0.17$, $P > 0.5$) and years of education (CB mean = 16.9, SD = 2.6; S mean = 18.1, SD = 2.62, $t(21) = 1.2$, $P = 0.2$). Data from 1 additional blind participant were excluded because after the scan they reported temporarily having vision during childhood.

Table 1. Participant count by etiology of blindness.

Etiology	Participant number
Leber congenital amaurosis	7
Retinopathy of prematurity	8
Optic nerve hypoplasia	3
Retinitis pigmentosa	1
Unknown	3

At the time of the study, participants were not taking psychoactive medications, by self-report, and reported no history of neurological disorders, brain damage, or head injuries. For blind participants, all causes of blindness were due to damage in areas posterior to the optic chiasm, such as the eye or optic nerve, and not brain damage (Table 1). All participants provided informed consent as approved by the Johns Hopkins Institutional Review Board. A subset of these data has been reported in previous analyses (cf. Loiotile et al. 2019).

Stimuli

The main testing materials consisted of 6 audio clips each lasting 5–7 min. Three of the audio clips were excerpts from popular live action movies. These sound clips were selected to facilitate a shared interpretation and experience across participants, because they are suspenseful, engaging, and easy to follow. The remaining 3 audio clips were each created from the same 6-min excerpt of a live comedy sketch, “Pie-Man.” The intact version of Pie-Man was presented in its original format. The “Sentence-Shuffle” version was created by splicing and reordering the sentences of the intact version, such that the clip contained intelligible sentences but lacked a coherent plotline. Finally, the “Backwards Speech” version was created by playing the clip in time-reverse format, such that it lacked any intelligible content (cf. Loiotile et al. 2019). The intact, scrambled, and time-reversed versions of “Pie-Man” have been used in several previous neuroimaging studies to probe shared brain responses across sighted individuals (e.g. Lerner et al. 2011; Stephens et al. 2013; Simony et al. 2016). We also collected a resting-state scan, during which no auditory stimuli were presented and participants were instructed to relax and stay awake. All stimuli are available for download at the Open Science Framework: <https://osf.io/r4tgb/> (Table 2)

Procedure

Participants passively listened to each sound clip during fMRI scanning. Each clip was assigned to a separate scanning run and clips were presented in a pseudorandom order to each participant, such that the sequence for each blind participant was yoked to a corresponding sighted participant. For each “intact” stimulus, participants were read a 2–3 sentence prologue that provided context for the upcoming sound clip immediately before the scanning run began. Participants were instructed to

Table 2. Description of the main auditory stimulus conditions.

Stimulus name	Condition	Duration (min)	TR	RMS amplitude	Frequency (Hz)	Blind subjects	Sighted subjects
Rest	Non-intact	7.4	240			22	21
Backwards Speech	Non-intact	6.8	223	0.032	1,177	22	22
Sentence-Scramble	Non-intact	6.8	223	0.032	1,177	22	22
Pie-Man	Intact	6.8	223	0.032	1,177	22	22
Movie 1 (<i>The Conjuring</i>)	Intact	5.1	172	0.11	2,472	22	22
Movie 2 (<i>Taken</i>)	Intact	5	169	0.031	1,600	22	21
Movie 3 (<i>Blow-Out</i>)	Intact	6.5	215	0.054	4,414	22	22

listen carefully and pay attention, as they would later be asked questions about the story content of each clip. The presentation of each auditory clip was preceded by 5 s of rest and followed by 20–22 s of rest. These rest periods were not included in the analyses. All participants wore light exclusion blindfolds during scanning. All participants completed all 7 scanning runs, except for 1 sighted participant who did not complete 1 audio-movie scanning run and the resting-state scan due to time constraints.

Prior to scanning, we confirmed that each participant was not already familiar with the intact clips (i.e., they had not previously seen the movies that the clips were sourced from). After completing the fMRI scans, participants exited the scanner and immediately answered 5 orally presented multiple choice questions for each of the intact auditory clips (see [Supplementary Table S2](#)). We included data from all participants in all reported brain analyses (see [Supplementary Table S1](#) for comprehension scores by group and condition). However, results are qualitatively similar when analyses are limited to data from participants who scored 3/5 or better on all 4 post-scan comprehension tests (see [Supplementary Figs S10 and S11](#)).

Auditory stimuli were presented over Sensimetrics MRI-compatible earphones (<http://www.sens.com/products/model-s14/>) at the maximum comfortable volume for each participant. Prior to the main stimulus presentation and during the acquisition of the structural scans, we tested participants' ability to hear sounds over the scanner noise. Volume levels were adjusted to maximize audibility and comfort (cf. [Loiotile et al. 2019](#)).

fMRI data acquisition

Structural and functional MRI data of the whole brain were collected on a 3 Tesla Phillips scanner. T1-weighted structural images were collected in 150 axial slices with 1 mm isotropic voxels using a magnetization-prepared rapid gradient echo. T2*-weighted functional images were collected with a gradient echo planar imaging sequences in 36 sequential ascending axial slices with $2.4 \times 2.4 \times 3$ mm voxels and 2-s time repetition (TR; echo time: 30 ms, flip angle: 70°, field-of-view: 76×70 matrix, slice thickness: 2.5 mm, inter-slice gap: 0.5,

slice coverage: FH 107.5, PH direction L/R, first-order shimming).

fMRI preprocessing

Preprocessing was performed using FEAT (fMRI Expert Analysis Tool) Version 6.00, part of FSL (<http://fsl.fmrib.ox.ac.uk/fsl/>) and included slice time correction using Fourier space time-series phase-shifting, motion correction using MCFLIRT ([Jenkinson et al. 2002](#)), high-pass filtering (140 s), and linear detrending. All functional volumes were co-registered and affine transformed to a standard anatomical brain (MNI152) using FLIRT. Functional data were smoothed with a 4-mm full-width at half-maximum Gaussian kernel and resampled to 3 mm isotropic voxels. The first 4 and last 8 TRs of each scanning run were discarded, corresponding to the rest periods before and after the clips (accounting for delays in hemodynamic response). Analyses were performed in volume space and data were projected onto a cortical surface with the HCP Workbench for visualization ([Marcus et al. 2011](#)).

Inter-subject pattern similarity analysis

We computed spatial pattern inter-subject correlations (spatial ISC) for each subject group (blind and sighted) and condition (Audio-Movies, Pie-Man, Sentence-Shuffle and Backwards Speech) ([Chen et al. 2017](#); [Nastase et al. 2019](#); [Zuo et al. 2020](#)). Pattern analysis was conducted in each of 400 parcels from an independent whole-brain resting-state parcellation ([Fig. 1C](#)) ([Schaefer et al. 2018](#)). For each run, time-series data were divided into a set of nonoverlapping 10-s segments (32–47 segments per run) and averaged across TRs within a segment, yielding one brain activity pattern for each segment in each parcel ([Fig. 1A](#); see [Supplementary Fig. S1](#) for example segment-level patterns). Within each parcel, the Pearson correlation was calculated between every segment pattern for each participant versus every segment pattern averaged across the remaining participants, yielding a segment-by-segment correlation matrix ([Fig. 1B](#)). The spatial ISC value is computed by averaging together the on-diagonal (i.e., matching) segment pattern similarity values. For the Audio-Movies condition, data from all 3 audio-movie clips were concatenated together prior to computing spatial ISC. The Audio-Movies analysis was limited to

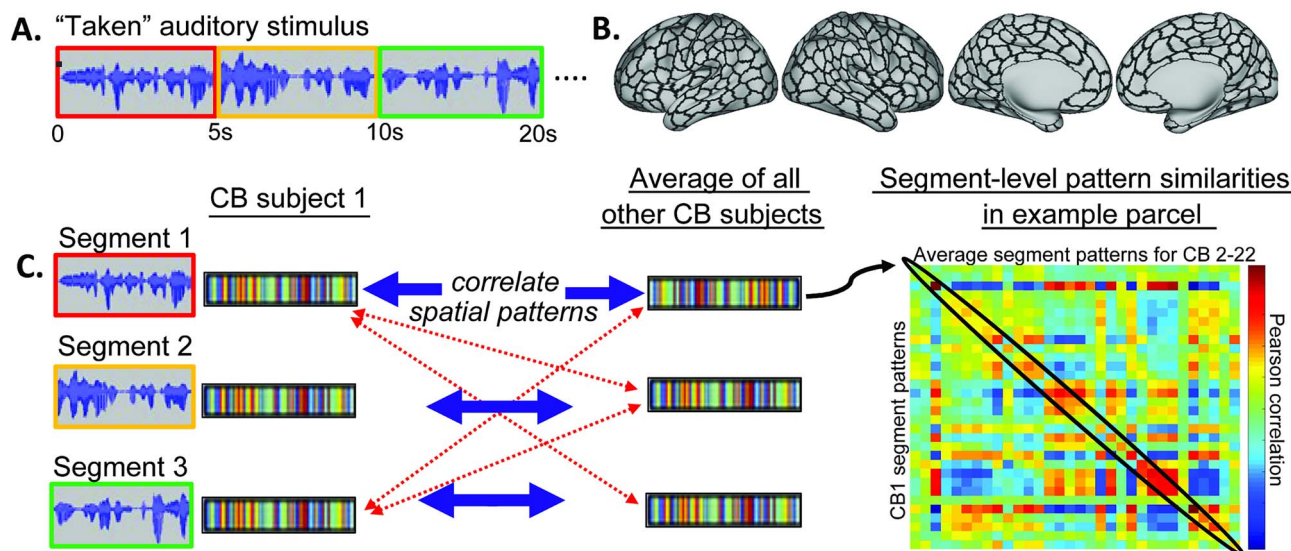


Fig. 1. Analysis schematic of spatial pattern ISC analysis. A) Each stimulus was segmented into 10-s long segments. B) Similarities were computed between one subject's segment-level spatial patterns (CB 1) and the group-average patterns from the remaining members of their respective group (CB 2–22). The mean on-diagonal segment pattern similarity (circled) provides the spatial ISC value. C) Group-average spatial ISC values were computed in each of 400 parcels for each auditory stimulus. Parcellation was determined by a resting-state analysis on independent data (Schaefer et al. 2018).

participants who had usable data for all 3 movie clips (CB $n = 22$, $S n = 21$). Results for each individual audio-movie stimulus are presented in [Supplementary Materials](#).

Group-level spatial ISC values were computed by averaging the ISC values across segments and across participants. To determine statistical significance, the observed group-level spatial ISC values were compared to permutation-based null distributions. For each parcel, a null distribution was generated by randomly shuffling the spatial ISC values in the group-average segment-by-segment pattern correlation matrix (Fig. 1B) 1,000 times and retaining the group-average mean on-diagonal value of each resulting similarity matrix (Kriegeskorte 2008). This resulted in 1,000 parcel ISC maps derived from scrambled spatial ISC values. From each null parcel map generated from this permuted data, the largest of the 400 spatial ISC parcel values was retained, yielding a null distribution of 1,000 maximum noise correlation values (cf. Regev et al. 2013). Family-wise error rate was then defined as the top 5% of the null distribution of the maximum correlation values, which was used to threshold the observed parcel map (Nichols and Holmes 2002). This analysis ensures that the patterns in above-threshold parcels contain segment-specific information, because the average correlation between spatial patterns for matching segments must exceed an equal-sized random sample of correlations between all segments (i.e., both matching and nonmatching) in order to meet statistical significance (cf. Chen et al. 2017).

Between-condition comparisons

To identify parcels where spatial ISC was reliably greater for one stimulus condition versus another, we computed a condition difference score for each participant (e.g. Audio-Movies spatial ISC minus Backwards Speech

spatial ISC) and then averaged these scores across participants. To generate a null distribution, at each parcel, we randomly flipped the sign on the difference score for a random subset (half) of the participants before computing the group-average difference value (cf. Aly et al. 2018). This procedure was repeated 1,000 times at each parcel to generate a null distribution of null difference values. As there were several parcels where the observed group differences in spatial ISC values exceeded all null values, P-values (one-tailed) were estimated for all parcels by using the null distribution's mean and standard deviation to fit a normal distribution, allowing P-values to be calculated even when the observed differences in spatial ISC values for a parcel exceeded all null values. To correct for multiple comparisons across parcels, we controlled the false discovery rate (FDR) (Benjamini and Hochberg 1995) using an FDR threshold of $q = 0.05$. The observed group-average difference value (i.e., without any flipped signs) was then compared against this null distribution. For both statistical thresholding and visualization, each between-condition comparison was limited to parcels that showed reliable within-condition spatial ISC for either of the 2 conditions being compared (Chen et al. 2017). For the comparison Audio-Movies minus Backwards Speech, similar results are observed when stimulus duration is matched across conditions (Supplementary Fig. S3).

Between-group comparisons

The group-average ISC value for the sighted participants was subtracted from the group-average spatial ISC value for the blind group, yielding a CB-S difference score. To determine statistical significance, a null distribution of 1,000 difference scores was generated by shuffling the labels of each subject's group membership prior

to computing each group-average ISC value and then computing the CB-S difference score based on the randomly labeled data. This procedure was repeated 1,000 times at each parcel, and the true CB-S difference score (i.e., the resulting value when group membership labels were correctly assigned) was compared to this null distribution, yielding one P-value (one-tailed) per parcel. FDR correction for multiple comparisons ($q = 0.05$) was then applied to threshold the resulting P-values. To identify parcels where between-condition contrasts differ between groups, this procedure was performed on within-subject spatial ISC difference scores (e.g. Audio-Movies – Backwards Speech) rather than on the raw spatial ISC values themselves. For both statistical thresholding and visualization, each between-group comparison was limited to parcels that showed reliable within-condition spatial ISC for either of the 2 subject groups.

Results

Audio-Movies induce shared patterns in higher cognitive regions in both groups, relative to Backwards Speech

Backwards Speech elicited reliable shared spatial patterns (spatial ISC) in auditory cortices across individuals for both blind and sighted groups. In addition, shared patterns were observed for the blind group in the right lateral and orbital frontal cortex, left precuneus, and left superior extrastriate cortex. A direct comparison of the 2 groups did not reveal any parcels where spatial ISC values for the blind exceeded the sighted. There were no differences between the 2 groups in the visual cortices (Fig. 2A). As expected, resting-state stimuli did not elicit shared spatial patterns anywhere in the brain for either group.

Audio-Movies elicited reliable shared spatial patterns not only in auditory cortices but also in higher cognitive networks, including large segments of lateral temporal and prefrontal cortices, and the precuneus for both groups (Fig. 2B). For both blind and sighted groups, higher cognitive networks showed reliably greater spatial ISC in response to the Audio-Movies as compared to Backwards Speech (Fig. 2C).

Audio-Movies induce shared spatial patterns in visual cortices of blind participants

For the blind group, Audio-Movies elicited significant inter-subject spatial pattern correlations in occipital and OT areas, including bilateral V1, bilateral lingual gyrus, right-lateralized posterior fusiform gyrus, and inferior OT cortex. In the sighted group, occipital involvement was less extensive. However, the part of occipital cortex directly ventral to the precuneus and one parcel in the left occipital pole also showed reliable spatial ISC in the sighted group.

When blind and sighted groups were compared to each other directly, a subset of occipital regions with

reliable spatial ISC for Audio-Movies in the blind group also showed significantly larger ISC in blind relative to sighted people. Spatial ISC was higher for Audio-Movies among blind people in ventral OT cortex, right lingual gyrus, right OT cortex, and the right occipital pole, as well as medially in left V1 and V2 (Fig. 2B). Right OT cortex and bilateral medial lingual gyrus also showed a significant group-by-condition interaction: blind > sighted, Audio-Movies > Backwards Speech (Fig. 2C). In addition to these visual regions, spatial ISC increased for Audio-Movies versus Backwards Speech in the blind group, relative to the sighted, in the temporoparietal junction and lateral prefrontal cortex bilaterally, in the right auditory cortex, and in the left anterior cingulate cortex. Spatial ISC maps for each individual stimulus condition are shown in [Supplementary Fig. S2](#).

As noted in Section 1, a previously published analysis of these data tested for synchronized timecourses across subjects over the duration of each stimulus condition (i.e., temporal ISC instead of spatial ISC in the current study, cf. [Loiotile et al. 2019](#)). To compare the current spatial ISC results to the previous temporal ISC analysis, with the same dataset, we plotted spatial ISC values (y-axis) as a function of temporal ISC values (x-axis) (Fig. 3) for Audio-Movies and Backwards Speech conditions and for each subject group. Each dot in the plot represents a single parcel. Parcels located in visual cortices are shown in gray (Visual Network from [Schaefer et al. \(2018\)](#) 17-Network Parcellation). In both groups and conditions, temporal ISC values (x-axis) are greater than spatial ISC values (y-axis), but the 2 measures are correlated across parcels. In the blind relative to the sighted group, the visual parcels shift right for the Audio-Movies condition, reflecting higher temporal ISC, and a subset of these visual parcels also shift upward, reflecting higher spatial ISC. For direct comparisons of spatial and temporal ISC values in the blind group versus the sighted group, see [Supplementary Fig. S7](#).

Spoken narrative (Pie-Man) and sentences elicit shared spatial patterns in the visual cortices of blind but not sighted individuals

Results for the Pie-Man spoken narrative stimulus were qualitatively consistent with those observed in response to the Audio-Movie stimuli in both groups; however, Pie-Man responses were weaker ([Supplementary Fig. S5](#)). In both groups, Pie-Man elicited shared spatial patterns in bilateral auditory cortex, bilateral medial prefrontal cortex, bilateral lateral temporal cortex, and precuneus. A direct comparison of the 2 groups revealed that Pie-Man elicited greater spatial ISC in the blind group in several visual cortex parcels, including bilateral medial visual cortex and right occipital pole, as well as a left lateral prefrontal cortex parcel ([Supplementary Fig. S4](#)). Spatial ISC in right anterior temporal pole was greater among the sighted group.

The Sentence-Shuffle stimuli induced spatial ISC in similar areas in both groups, including bilateral auditory

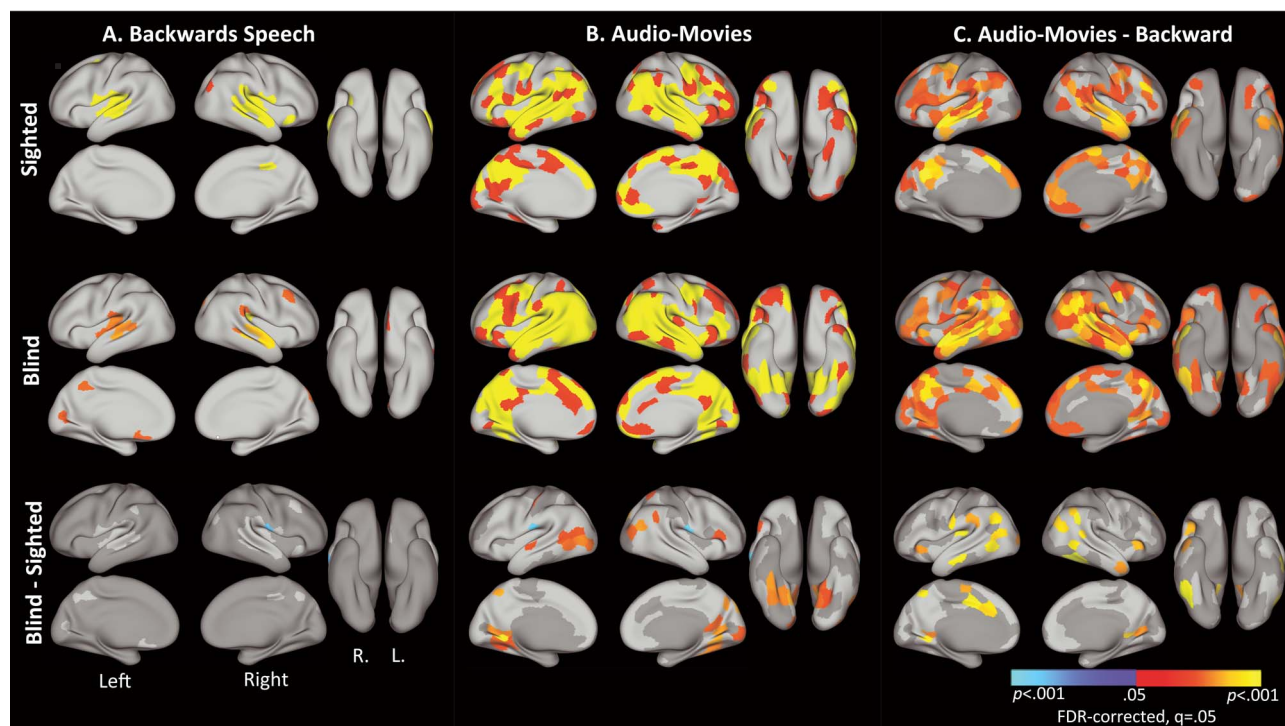


Fig. 2. Parcels with reliable spatial pattern inter-subject correlation values both within- (sighted, top row; CB, middle row) and between-subject groups (CB versus sighted, bottom row) for A) the Backwards Speech condition, B) the Movies condition, and C) the contrast of Audio-Movies versus Backwards Speech. Maps for each individual stimulus condition are shown in [Supplementary Figs S2 and S3](#). All maps corrected for multiple comparisons, $P < 0.05$. Between-group comparisons (bottom row) are limited to parcels with above-threshold spatial ISC for either group, and between-condition comparisons (column C) are limited to parcels with above-threshold spatial ISC for either condition. (Dark gray: excluded parcels; light gray: included parcels, below threshold; colored parcels: included parcels, above threshold).

cortex and bilateral lateral temporal cortex. Blind people showed greater spatial ISC than the sighted for Sentence-Shuffle condition in the right temporoparietal junction and one parcel in left medial visual cortex.

In both groups, spatial ISC was greater for Pie-Man versus the Sentence-Shuffle condition in several nonvisual brain areas bilaterally, including medial prefrontal cortex, lateral temporal cortex, and precuneus. In the blind but not the sighted group, spatial ISC was greater for Pie-Man versus Sentence-Shuffle in several occipital regions, including those that showed reliable spatial ISC in response to the Audio-Movies ([Supplementary Fig. S6](#)). Two of these visual cortex parcels were also significant in a group-by-condition interaction test (blind > sighted, Pie-Man > Sentence Shuffle): one on the right occipital pole and one on the left anterior OT cortex.

Discussion

We observed segment-specific spatially distributed patterns of activity in the “visual” cortices of blind individuals in response to naturalistic auditory narratives. The spatial organization of these responses was similar across different blind individuals, such that direct comparisons of multivoxel activity patterns across people revealed alignment in several regions of the occipital lobes, including medial and foveal V1 as well as

regions in ventral OT cortex. These findings suggest that information is spatially distributed within the visual cortices of different blind people in a consistent way. While we also observed some evidence of shared spatial patterns in the visual cortices of sighted individuals, the robustness and spatial extent of this effect were greater in the blind group.

The shared spatial patterns in visual cortex emerged in response to the meaningful naturalistic sound clips but not unintelligible Backwards Speech. The naturalistic sound clips used in the current study were expressly designed to entertain viewers with complex and interdependent events and characters. Unlike Backwards Speech, the movie sound clips feature plot lines that build over time, spoken language dialogues; music and emotive tones; environmental sounds; and auditory cues to movement. The current results suggest that visual cortices of people born blind are sensitive to such meaningful content.

Importantly, patterns of activity within visual cortices of people who are blind are sensitive to information that varies over the duration of each audio-movie clip. In order for a brain region to yield a statistically robust spatial ISC value, each 10-s audio-movie segment must, on average, show reliably greater pattern similarity across people for matching segments versus mismatching segments. Thus, not only are visual cortices sensitive to the difference between auditory movies and Backwards Speech, but

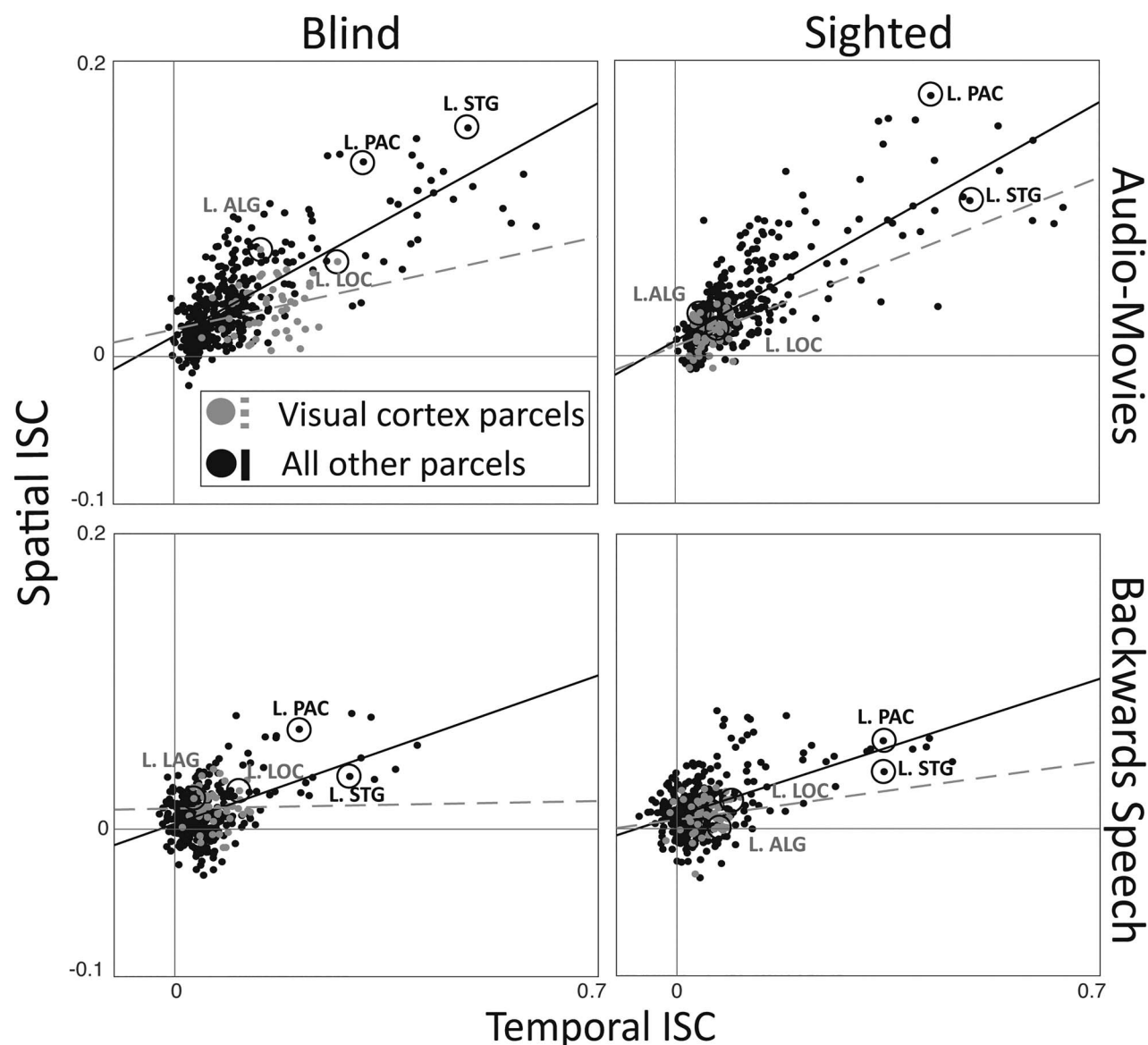


Fig. 3. Scatterplots depicting ISC values (spatial ISC versus temporal ISC) in each of the 400 parcels, separated by subject group and stimulus condition. Anatomical labels for example brain regions correspond to the nearest circled parcel dot. Gray dots show parcels located in the visual network as identified in the [Schaefer et al. \(2018\)](#) 17-Network brain parcellation and black dots depict all other parcels. Trend lines depict the linear relationships between spatial and temporal ISC for each subject group and stimulus condition (visual cortex parcels: dashed line; all other parcels: solid line). Note that spatial and temporal ISC axes are shown on different scales as temporal ISC values are larger than spatial ISC values. Spatial and temporal ISC values are more correlated in the Audio-Movies stimuli than in the Backwards Speech, particularly for parcels outside of the visual cortex (Audio-Movies: Blind, visual parcels $r = 0.25$, nonvisual parcels $r = 0.76$; Sighted, visual parcels $r = 0.34$, nonvisual parcels $r = 0.77$; Backward Speech: Blind, visual parcels $r = 0.02$, nonvisual parcels $r = 0.48$; Sighted, visual parcels $r = 0.14$, nonvisual parcels $r = 0.50$). L, left; STG, superior temporal gyrus; PAC, primary auditory cortex; LOC, lateral occipital complex; ALG, anterior lingual gyrus.

they are also sensitive to differences among different segments of a given audio-movie.

The current study suggests sensitivity to the meaningful content of naturalistic auditory narratives in visual cortices of people born blind. However, it does not provide definitive insight into the specific cognitive information that engages deafferented visual cortices. We also cannot rule out the contribution of attention to the observed effects. In addition to having meaningful content, Audio-Movies and narratives are inherently more engaging than meaningless Backwards Speech stimuli. Increased attention while listening to the narratives,

relative to unintelligible speech, could drive larger and more robust activity, which in turn could lead to better detection of common spatial patterns across people. Future studies will need to investigate precisely what aspects of naturalistic audio clips elicit shared spatial patterns within the visual cortices of people born blind. To test the hypothesis that visual cortices of people born blind are sensitive to the meaning conveyed by naturalistic audio-clips, one could manipulate the meaning extracted without changing the stimulus. One approach would be to measure shared brain responses to semantically ambiguous narrative that could be interpreted in

2 distinct ways, after biasing 2 separate groups of blind participants toward each interpretation (cf. Yeshurun et al. 2017; Finn et al. 2018). If visual cortices are sensitive to the semantic content of meaningful naturalistic sound clips, spatial ISC should be high within-group and low between groups during moments in a narrative when the 2 interpretations diverge between groups, despite the input stimulus and attentional demands being identical for both groups. Controlled experiments can also test for multivariate sensitivity to specific types of high-level cognitive content (e.g. narrative meaning) and dissociate it from attentional effects. Since the function of “visual” cortices in people born blind is not known, we cannot rule out the possibility that other stimuli or tasks would be better at eliciting “visual” cortex maps in this population.

Outside of visual cortex, several additional brain regions also showed consistent spatial patterns during meaningful auditory clips relative to Backwards Speech in both the blind and sighted groups. Consistent with previous findings in sighted people, high spatial ISC emerged in several brain regions associated with higher cognitive processing, including precuneus, medial frontal cortex, and bilaterally in the lateral frontal cortex and lateral temporal cortex. These areas are thought to support linguistic, semantic, and social processes (Hassabis et al. 2007; Buckner et al. 2008; Binder et al. 2009; Fedorenko et al. 2011). Largely similar meaning-sensitive regions emerged across blind and sighted groups, consistent with previous evidence that lack of vision does not substantially alter the organization of the semantic system (e.g. Bedny et al. 2012; Handjaras et al. 2017; Bottini et al. 2020). We observed a similar response profile in “visual” cortices of blind people and high-level semantic networks of sighted and blind adults alike. One possibility therefore is that in blindness, the visual cortices assume functions similar to those performed in higher cognitive frontal, temporal, and parietal networks in both sighted and blind people. However, more work is needed to determine the extent to which content is redundant across distinct brain regions that exhibit shared segment-level spatial patterns.

Outstanding questions also concern the spatial scale and the inter-individual variability of “visual” cortex representations in blindness. Our results build on previous univariate ISC analyses, reporting that “visual” cortices of different blind participants aligned in temporal activity in response to narrative auditory stimuli (i.e., temporal ISC) (Van Ackeren et al. 2018; Loitile et al. 2019). Extending these prior findings, we report that people born blind develop spatially distributed representations within visual cortices that are cognitively fine-grained enough to differentiate between 10-s subsegments of naturalistic auditory excerpts and are spatially similar across different people. Temporal (univariate) ISC and spatial (multivariate) ISC results generally align. However, due to its lower statistical power, spatial

(multivariate) ISC was reduced relative to temporal (univariate) ISC throughout the cortex for both groups. Interestingly, reduced spatial relative to temporal ISC was particularly pronounced in visual cortices of the blind group. In other words, relative to the sighted, the blind group showed larger increases in temporal (univariate) than spatial (multivariate) occipital ISC (i.e., in Fig. 3, visual cortex parcels of the blind group are shifted further right than upward, relative to the sighted). Prior work has found that, in sighted people, spatial ISC is highly robust in occipital cortices during visual stimulation, making it unlikely that the greater reduction of spatial versus temporal ISC in occipital cortex of the blind group in the current study is due to intrinsic occipital cortex physiology (Chen et al. 2017). In one such paper, spatial ISC in occipital areas during movie viewing was approximately $r = 0.3$ (see Supplementary Fig. 3B in Chen et al. (2017)). In the current data, we find that spatial ISC in visual cortex for the blind group is around $r = 0.03$ – 0.05 for the Audio-Movies, whereas spatial ISC in the precuneus $r = 0.05$ – 0.07 . In future work, presenting the same naturalistic stimuli to the same blind participants multiple times could test whether occipital maps are more variable across different blind people or less spatially segregated within each individual blind person. Such analyses might reveal even more fine-scale representations that are sensitive to segment-specific patterns within person but are different across individuals.

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Supplementary material

Supplementary material is available at Cerebral Cortex online.

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