

000  
 001  
 002  
 003  
 004  
**END-TO-END TOPOGRAPHIC AUDITORY MODELS**  
**REPLICATE SIGNATURES OF HUMAN AUDITORY COR-**  
**TEX**

005  
 006 **Anonymous authors**  
 007 Paper under double-blind review  
 008  
 009  
 010  
 011

012 **ABSTRACT**

013 The human auditory cortex is topographically organized. Neurons with similar  
 014 response properties are spatially clustered, forming smooth maps for acoustic features  
 015 such as frequency in early auditory areas, and modular regions selective for  
 016 music and speech in higher-order cortex. Yet, evaluations for current computa-  
 017 tional models of auditory perception do not measure whether such topographic  
 018 structure is present in a candidate model. Here, we show that cortical topography  
 019 is not present in the previous best-performing models at predicting human auditory  
 020 fMRI responses. To encourage the emergence of topographic organization, we  
 021 adapt a cortical wiring-constraint loss originally designed for visual perception.  
 022 The new class of topographic auditory models, TopoAudio, are trained to classify  
 023 speech, and environmental sounds from cochleagram inputs, with an added con-  
 024 straint that nearby units on a 2D cortical sheet develop similar tuning. Despite  
 025 these additional constraints, TopoAudio achieves high accuracy on benchmark  
 026 tasks comparable to the unconstrained non-topographic baseline models. Further,  
 027 TopoAudio predicts the fMRI responses in the brain as well as standard models,  
 028 but unlike standard models, TopoAudio develops smooth, topographic maps for  
 029 tonotopy and amplitude modulation (common properties of early auditory repre-  
 030 sentation, as well as clustered response modules for music and speech (higher-  
 031 order selectivity observed in the human auditory cortex). TopoAudio is the first  
 032 end-to-end biologically grounded auditory model to exhibit emergent topography,  
 033 and our results emphasize that a wiring-length constraint can serve as a general-  
 034 purpose regularization tool to achieve biologically aligned representations.

035 **1 INTRODUCTION**

036  
 037 The human auditory cortex has a well documented *topographic* organization in which neurons with  
 038 similar response properties are spatially clustered (Moerel et al., 2014; Brewer & Barton, 2016;  
 039 Scheich, 1991; Kanold et al., 2014; Read et al., 2002; Leaver & Rauschecker, 2016). In early  
 040 auditory areas, this organization gives rise to smooth topographic maps for acoustic features such  
 041 as frequency (tonotopy), amplitude modulation, and pitch (Reale & Imig, 1980; Bendor & Wang,  
 042 2005; Wessinger et al., 1997; Allen et al., 2022; Joris et al., 2004; Baumann et al., 2015; Norman-  
 043 Haignere et al., 2013). In higher-order regions, distinct clusters emerge for more complex categories  
 044 like music and speech (Zatorre et al., 2002; Leaver & Rauschecker, 2010; Norman-Haignere et al.,  
 045 2015; 2022; Harris et al., 2023; Williams et al., 2022; Fedorenko et al., 2012; Boebinger et al.,  
 046 2021). In recent years, computational models have emerged that capture key aspects of human  
 047 auditory behavior (Francl & McDermott, 2022; Saddler et al., 2020; 2021; Saddler & McDermott,  
 048 2024; Koumura et al., 2023) and predict neural responses (Kell et al., 2018; Tuckute et al., 2023;  
 049 Giordano et al., 2023; Güçlü et al., 2016; Khatami & Escabí, 2020; Vaidya et al., 2022; Millet et al.,  
 050 2022; Rupp et al., 2025). Yet even the leading models of the auditory cortex (Tuckute et al., 2023)  
 neither incorporate, evaluate, nor explain the topography observed in the brain.

051 To develop such models, we take inspiration from recent work that utilizes wiring-length constraints  
 052 to induce topographic structure. One compelling hypothesis for the ubiquitous nature of corti-  
 053 cal maps is that they emerge from optimizing task representations under wiring-length constraints  
 (Kaas, 1997; Chklovskii & Koulakov, 2004; Jacobs & Jordan, 1992). If wiring-length indeed serves

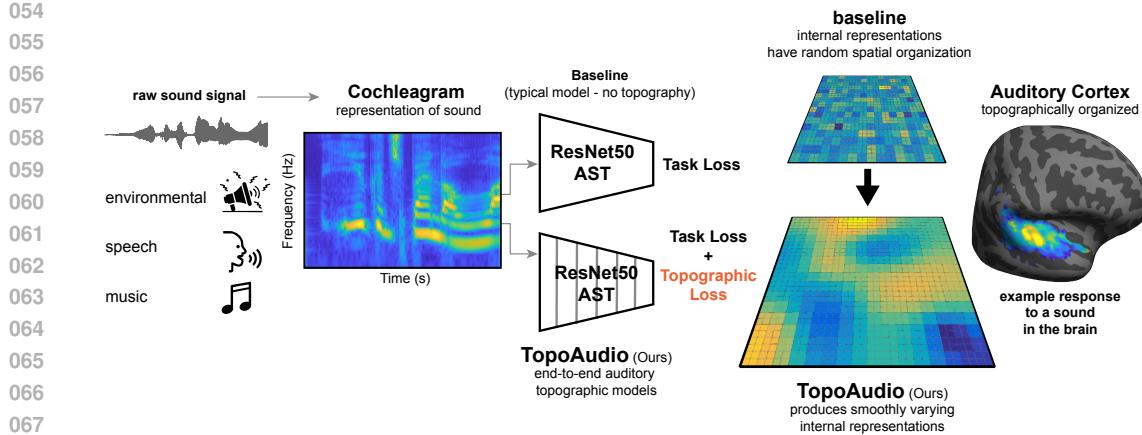


Figure 1: **TopoAudio: Topographic audio models.** Raw sound waveforms are transformed into cochleograms, which serve as inputs to the neural network backbone (middle). The baseline model (middle, top) is trained using only a task loss and learns spatially disorganized internal representations. In contrast, our proposed model TopoAudio is trained with an additional spatial smoothness constraint via TopoLoss. This results in smooth, topographically organized representations that resemble those observed in human auditory cortex (right).

as a domain-general principle in neural representation, then it should suffice to capture cortical maps in any modality. This principle was recently implemented in vision models Lee et al. (2020); Margalit et al. (2024); Qian et al. (2024); Deb et al. (2025), where a wiring-length constraint led to an emergence of topographic information and a better alignment with neural data. More recently, in attempt to show generality, a wiring-length constraint was applied to language models (Rathi et al., 2025; Deb et al., 2025), however the overall topography of core language regions in the biological brain is debated, so it is unclear if these results lead to a more biological model. The auditory domain is a natural test of this wiring-length hypothesis – it encodes dynamic features, and has some known topographic structure.

In this work, we present **TopoAudio**, the first suite of end-to-end topographic auditory models. Our models achieve competitive performance at predicting fMRI responses in the human auditory cortex and perform at par with baseline models on auditory classification tasks. Beyond these standard evaluations, we further investigate if the wiring-length constraint leads to hallmark features of auditory cortical organization: smooth tonotopic and modulation maps, and spatially clustered regions selective for speech and music. We find that the internal representations of TopoAudio models are more geometrically aligned with human brain data than standard models, demonstrating that incorporating topographic structure yields models that are both high-performing and biologically grounded. Our TopoAudio models provide strong evidence of a domain-general principle for introducing topography into AI models, enabling them to capture the emergence of spatial organization in any modality.

## 2 RELATED WORKS

### 2.1 TOPOGRAPHIC MODELS IN VISION AND LANGUAGE.

Topography is ubiquitous across sensory cortices. Perhaps the best known example is the visual cortex, where in early visual cortex neurons are arranged in fine-scale maps for orientation preference (Blasdel, 1992) - forming structured motifs such as pinwheels. At larger scales, cortical maps exhibit biases for real-world properties like object size, animacy (Konkle & Oliva, 2011; Konkle & Caramazza, 2013), and eccentricity, including specialized regions selective for faces, bodies, scenes, and words (Kanwisher, 2000; Grill-Spector et al., 2004; Epstein et al., 1999; Downing et al., 2006; 2001; McCandliss et al., 2003). These observations from the brain have inspired the development of topographic deep learning models that jointly optimize for local similarity on internal represen-

108 tations along with task performance (Lee et al., 2020; Margalit et al., 2024; Qian et al., 2024; Deb  
109 et al., 2025).

110 There are broadly three approaches to inducing topography in neural networks during training. The  
111 first involves models like TDANNs, which promote spatial topography by encouraging distance-  
112 dependent response similarity using an exponential falloff function, mimicking the spatial corre-  
113 lation function obtained from experimental recordings from high-level visual cortex (Lee et al., 2020;  
114 Margalit et al., 2024). The second approach relies on lateral interactions, where nearby units are  
115 encouraged to perform similar computations, as in LLCNNs and related architectures (Qian et al.,  
116 2024; Dehghani et al., 2024). The third approach, TopoNets, is inspired by early synaptic pruning  
117 and Turing patterns, promotes topography by encouraging nearby units to develop similar weights,  
118 leading to smooth tuning across a cortical sheet (Deb et al., 2025). Among the three strategies,  
119 TopoNets and TDANNs have been successfully applied to both convolutional networks and trans-  
120 formers, and have shown promise beyond vision, including in the language domain (Rathi et al.,  
121 2024; Deb et al., 2025; Binhuraib et al., 2025). In this work, we directly test whether topographic  
122 constraints constitute a domain-general organizing principle. Specifically, we show that topography,  
123 successfully transfers to audition, a fundamentally distinct domain that has never been tested before.  
124 This is a critical scientific test of whether the principles underpinning cortical topography are truly  
125 shared across the brain and can be leveraged for model interpretability.

126

## 127 2.2 TOPOGRAPHY IN AUDITORY CORTEX AND AUDITORY MODELS

128

129 The topographic organization of auditory responses begins in the periphery with frequency prefer-  
130 ences, or tonotopy, of auditory nerve fibers innervating the cochlea (Dallos et al., 1996). This tono-  
131 topic structure is inherited by later brain regions subcortically and cortically (Pantev et al., 1995;  
132 Leaver & Rauschecker, 2016). Functional and anatomical subfields for other stimulus attributes  
133 have been reported in other subcortical and cortical regions, such as maps of spatial location in owl  
134 auditory midbrain Knudsen & Konishi (1978), topographical organization of responses to amplitude  
135 modulated sounds (Joris et al., 2004; Baumann et al., 2015), and specific neural populations for  
136 speech, music, and song in human auditory cortex (Norman-Haignere et al., 2015; 2022).

137

138 Tonotopic organization has long been part of the standard input representation for auditory model  
139 training, with models trained on representations such as mel-frequency cepstral coefficients (Mer-  
140 melstein, 1976) and cochleograms (Glasberg & Moore, 1990; McDermott & Simoncelli, 2011) that  
141 enforce neighboring input channels to have similar frequency tuning (Slaney, 1998). Recent years  
142 have seen a surge of brain-like deep learning models of auditory cortex (Tuckute et al., 2023) trained  
143 to perform real-world auditory tasks such as speech or music recognition, often with a biologically  
144 inspired tonotopic front-end. These models have been shown to predict human behavior and neural  
145 responses with increasing accuracy (Kell et al., 2018; Giordano et al., 2023; Tuckute et al., 2023;  
146 Franc & McDermott, 2022; Koumura et al., 2023). However, the internal topographic structure of  
147 these models has been rarely evaluated beyond investigating hierarchical organization (Kell et al.,  
148 2018; Tuckute et al., 2023), that is, early layers of the models are shown to predict primary audi-  
149 tory cortex, and late layers of the models are shown to predict higher-order auditory areas. Our  
150 work develops evaluation procedures for measuring the presence of smooth topographic maps in the  
151 domains of audio frequency, amplitude modulation, speech, and music.

152

153

## 154 3 METHODS

155

### 156 3.1 SPATIAL LOSS

157

158 To investigate how topographic constraints shape auditory representations, we adapted the TopoLoss  
159 framework (Deb et al., 2025) to the auditory domain. As before, we define a 2D "cortical sheet"  
160 from convolutional layers in the auditory model on which to enforce topography. Each convolutional  
161 kernel in the model is mapped onto this sheet. For a convolutional layer with  $c_{\text{input}}$  input channels  
162 and  $c_{\text{output}}$  output channels, and a kernel size of  $k \times k$ , the weight tensor  $W \in \mathbb{R}^{c_{\text{output}} \times c_{\text{input}} \times k \times k}$  is  
163 reshaped into a cortical representation  $C \in \mathbb{R}^{h \times w \times d}$ , where  $h \times w = c_{\text{output}}$ , and  $d = c_{\text{input}} \cdot k \cdot k$ .

162 To encourage smoothness in the cortical sheet  $C^{h \times w \times d}$ , we apply a blurring operation that removes  
 163 high-frequency variations. We compute a blurred version  $C'$  of the cortical sheet using a downsample-  
 164 ing factor  $\phi_h = \phi_w = 3$  followed by upsampling:  
 165

$$\text{Blur}(X, \phi_h, \phi_w) = f_{\text{up}} \left( f_{\text{down}} \left( X, \frac{h}{\phi_h}, \frac{w}{\phi_w} \right), h, w \right) \quad (1)$$

169 The *TopoLoss* is then defined as the negative mean cosine similarity between the original and blurred  
 170 cortical maps:  
 171

$$\mathcal{L}_{\text{topo}} = -\frac{1}{N} \sum_{i=1}^N \frac{C_i \cdot C'_i}{\|C_i\| \|C'_i\|} \quad (2)$$

172 This encourages neurons with similar functions to be spatially clustered, enhancing topographic  
 173 organization. Finally, we integrate the *TopoLoss* with the primary task loss  $\mathcal{L}_{\text{training}}$  as:  
 174

$$\mathcal{L}_{\text{total}} = \mathcal{L}_{\text{training}} + \tau \cdot \mathcal{L}_{\text{topo}} \quad (3)$$

181 where  $\tau$  is a scaling coefficient controlling the influence of topographic regularization. Higher values  
 182 of  $\tau$  encourage stronger topographic organization.  
 183

### 3.2 TOPOAUDIO ARCHITECTURE AND TRAINING

185 **Architectures.** Our models are based on two state-of-the-art auditory neural network backbones:  
 186 CochResNet50 and the Audio Spectrogram Transformer (AST). We specifically selected these two  
 187 complementary architectures because they were shown to be the most accurate models of human  
 188 auditory cortex responses (Tuckute et al., 2023). CochResNet50 adapts the standard ResNet50 back-  
 189 bone (He et al., 2015) to operate on time–frequency cochleograms using 2D convolutions. The input  
 190 to the model is a single-channel cochleogram of shape (1, 211, 390), representing 211 frequency  
 191 bins across 390 time steps. For the CochResNet50, the topographic loss was applied to the sec-  
 192 ond convolutional layer within each residual block, promoting spatial smoothness and topographic  
 193 organization across successive hierarchical stages of the network.

194 AST, in contrast, leverages a transformer-based architecture to model audio spectrograms through  
 195 non-overlapping patches and global self-attention (Gong et al., 2021). In our adaptation, AST also  
 196 operates on cochleogram, ensuring architectural differences rather than input representation drive  
 197 performance differences. The topographic loss was applied to the first feed-forward projection layers  
 198 within each transformer block. All models were trained on 4×H200 NVIDIA GPUs using identical  
 199 multi-task objectives (see next section), ensuring a fair comparison across architectures.

200 **Training objective.** All TopoAudio models were trained on the Word-Speaker-Noise dataset  
 201 (Feather et al., 2019), which supports multi-task learning for (1) word recognition, (2) speaker iden-  
 202 tification, and (3) background noise classification. The dataset includes 230,356 speech clips across  
 203 793 word classes and 432 speaker identities, with class sampling designed to reduce overlap (no  
 204 more than 25% samples from any one word-speaker pair). Background audio was drawn from  
 205 718,625 curated AudioSet clips consisting of human and animal sounds, various musical clips, and  
 206 environmental sounds to ensure diverse and high-quality noise.

207 Training samples included speech-only, noise-only, and speech+noise mixtures, with augmentations  
 208 such as random cropping, RMS normalization, and variable SNR mixing (−10 dB to +10 dB). This  
 209 setup enabled supervised learning across all tasks with consistent preprocessing. This robust training  
 210 procedures makes it a strong test-bed for assessing how topographic constraints influence auditory  
 211 model organization and performance.

### 3.3 MODEL EVALUATIONS

212 We benchmarked the performance of models trained with and without topography across a range  
 213 of auditory domains: ESC-50 (Piczak, 2015) for environmental sound classification, NSynth (Engel

et al., 2017) for musical instrument classification, and Speech Commands (Warden, 2018) for word and speaker recognition. Lastly, we evaluated these models on human auditory cortex datasets such as NH2015 (Norman-Haignere et al., 2015) and B2021 (Boebinger et al., 2021).

### 3.3.1 ACCURACY

For ESC-50, which includes 2,000 environmental sound clips across 50 categories, we followed the standard five-fold cross-validation protocol. Representations were taken from the penultimate layer of each model (e.g., AvgPool for ResNet50, CLS token for transformer). Each 5-second ESC-50 clip was randomly cropped into five 2-second segments to match the model input duration. All five crops of a training clip were used as independent training samples. During evaluation, we applied majority voting across the five crops of each test clip to determine the predicted class label. We applied cross-validation over five regularization parameters ( $C = [0.01, 0.1, 1.0, 10.0, 100.0]$ ). The final accuracy was averaged over the five ESC-50 folds.

For NSynth, which consists of approximately 300,000 musical notes played by a variety of instruments, we focused on the task of instrument family classification. Each audio clip is 4 seconds long and labeled with one of 11 instrument families (e.g., strings, brass, keyboard). To match input requirements of our models, we used the first 2-second segment of each clip. Similar to the ESC-50 pipeline, representations were extracted from the final pooling layer of each pretrained model and used to train an SVM with similar choice of cross-validation. We adopted the official NSynth validation and test splits, training on the validation set and evaluating top-1 classification accuracy on the test set.

For Speech Commands v2, which contains approximately 100,000 1-second utterances of 35 spoken command words (e.g. yes, no, up, down). To ensure consistency with model’s input during training, each audio clip was zero-padded to 2-seconds. We extracted frozen representations from the final pooling layer and trained a linear SVM to classify the command labels. We followed the standard validation-test split provided by the dataset: the SVM was trained on the validation set and evaluated on the held-out test set. Accuracy was measured as top-1 accuracy across all 35 classes.

### 3.3.2 ESTIMATING SPATIAL TOPOGRAPHY: SMOOTHING

To quantify spatial topography in model representations, we used a smoothness score that compares the tuning similarity of spatially nearby model unit pairs to that of distant pairs (Margalit et al., 2024; Deb et al., 2025). Let  $x$  be a vector of pairwise tuning similarity values sorted in order of increasing cortical distance. The smoothness score  $S(x)$  is then defined as:

$$S(x) = \frac{\max(x) - x_0}{x_0} \quad (4)$$

where  $x_0$  is the tuning similarity for the closest unit pair, and  $\max(x)$  represents the highest similarity across all distances. This metric captures how much tuning similarity drops with increasing distance, with higher values indicating smoother topographic organization across the cortical sheet. Higher smoothness indicates that units with similar representations are spatially closer, reflecting stronger topographic structure.

### 3.3.3 ESTIMATING SELECTIVITY

To visualize the selectivity of model units for specific categories, we extracted layer-wise representations in response to annotated stimuli and applied a standard t-statistic-based measure. Specifically, for each target category  $c$ , we compared the distribution of activation values to those from other categories  $o$  using the following formula:

$$t = \frac{\mu_c - \mu_o}{\sqrt{\frac{\sigma_c^2}{N_c} + \frac{\sigma_o^2}{N_o}}} \quad (5)$$

Here,  $\mu$ ,  $\sigma$ , and  $N$  represent the mean, standard deviation, and number of samples for each category, respectively. This score reflects how strongly a unit differentiates the target category from others,

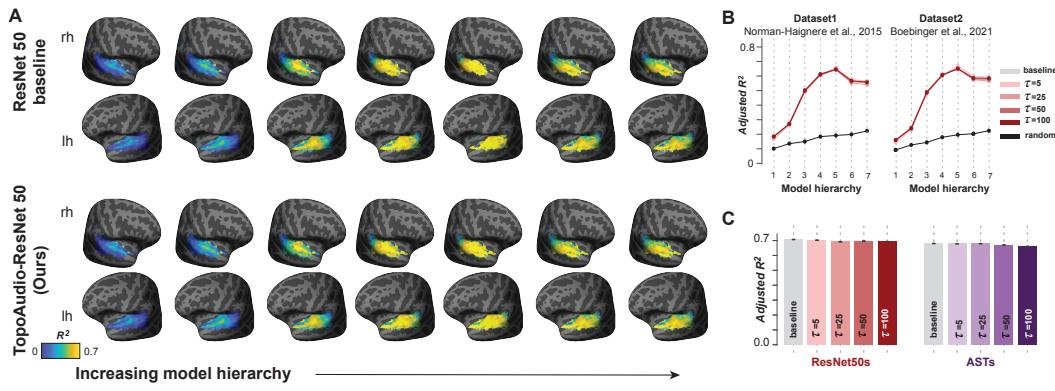


Figure 2: **Topographic auditory models maintain overall voxel-wise brain predictivity.** A) Brain maps display peak voxel-wise predictions across the auditory cortex for the baseline and topographic ResNet50. The colormap indicates the mean variance explained at each cortical vertex, averaged across subjects on the fsaverage surface. The model layers are shown from left to right, corresponding to increasing depth in the network hierarchy. B) ResNet50 model prediction accuracy as a function of depth in the network hierarchy for variants of the ResNet50 model on the NH2015 (Norman-Haignere et al., 2015) and B2021 (Boebinger et al., 2021) datasets. Note that the baseline model and the TopoAudio are highly overlapping. C) Bar plot summarizing peak encoding performance across all voxels for each model variant, including the random-initialized, baseline, and TopoAudio models for both the ResNet50 and AST architectures.

with higher values indicating greater selectivity. Layer maps are visualized by showing selectivity measured from each filter (for convolution-based models) or units (for transformer-based models) arranged on the 2D cortical sheet. When units with similar preferences cluster together spatially, the map appears smooth or patchy demonstrating topographic structure for the measured feature; when preferences are scattered, the map looks disorganized Figures 3 and 4.

### 3.3.4 FEATURES AND VOXEL DECOMPOSITION

Functional selectivities for speech and music are often not directly observable at the voxel level in fMRI data, and are instead inferred by decomposing voxel responses into a small number of latent components Norman-Haignere et al. (2015). To analyze the structure of model and brain responses, we adapted this voxel decomposition technique to the fMRI response matrix and model activations. Specifically, we adopted Non-parametric decomposition algorithm (Norman-Haignere et al., 2015), which factorizes a data matrix  $D \in \mathbb{R}^{S \times V}$  (where  $S$  for stimuli and  $V$  for voxels/features) into a response matrix  $R \in \mathbb{R}^{S \times N}$  and a weight matrix  $W \in \mathbb{R}^{N \times V}$  (where  $N$  for number of components), such that:

$$D \approx RW \quad (6)$$

This method is conceptually related to Independent Component Analysis (ICA), but differs in its approach to estimating non-Gaussianity. Instead of using contrast functions or kurtosis, it directly minimizes the entropy of the weight distribution using a histogram-based entropy estimator. This allows for the discovery of meaningful structure in high-dimensional data, including sparse or skewed distributions (Figure 4). This enabled us to extract shared components that capture interpretable spatial structure - such as tonotopic and category-selective regions. As has been shown in prior work, 6-components were sufficient to account for more than 80% of the noise-corrected variance in voxel responses (Norman-Haignere et al., 2015). Similarly, we adopted  $N = 6$  components for features and voxel decomposition.

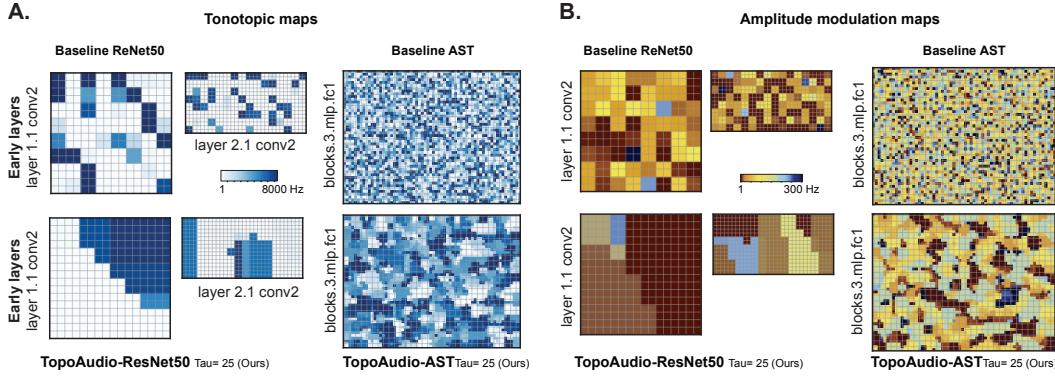


Figure 3: **TopoAudio models exhibit signatures of early auditory representations.** A) Tonotopic maps in baseline ResNet50s and ASTs (top row) are spatially disorganized, whereas TopoAudio models with topographic constraints ( $\tau = 25$  for ResNet50s,  $\tau = 5$  for ASTs; bottom row) exhibit smooth, spatially clustered frequency maps. B) Amplitude modulation tuning maps show a similar pattern: baseline models lack clear organization (top row), while topographic models (bottom row) develop coherent spatial clusters resembling auditory cortical maps.

## 4 RESULTS

### 4.1 TOPOAUDIO MODELS PRESERVE PERFORMANCE UNDER TOPOGRAPHIC CONSTRAINTS

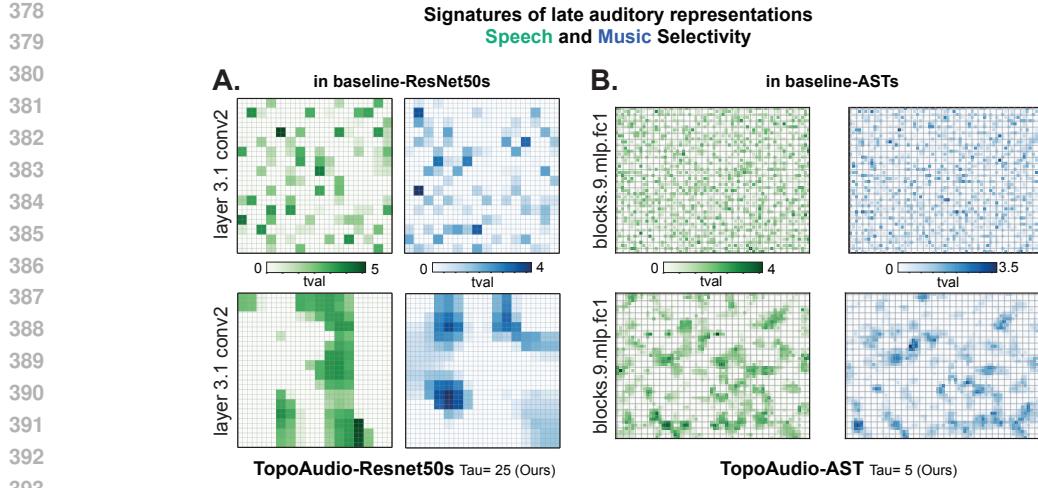
A typical concern with topographic neural network models is that introducing spatial constraints often leads to substantial drops in task performance on standard engineering tests (Qian et al., 2024). To examine whether this tradeoff holds in the auditory domain, we evaluated TopoAudio with varying levels of topographic smoothness (controlled by hyperparameter  $\tau$ ), against baseline non-topographic models on three benchmark datasets: environmental sounds, speech, and music (see section 3).

Appendix Table 1 shows the model performance accuracy for all models across each evaluation domain. Critically, despite the additional topographic constraint, all TopoAudio variants maintained high classification accuracy across tasks. Performance was consistently comparable to the non-topographic baseline model. These results demonstrate that topographic organization can be induced in auditory networks without sacrificing task performance, and establish TopoAudios as competitive auditory models suitable for further analyses.

### 4.2 TOPOAUDIOS PREDICT HUMAN FMRI RESPONSES WITH HIGH ACCURACY

A key requirement for any biologically inspired model is that it must retain strong predictive performance while better aligning with the structure of neural data. To assess whether brain predictivity is maintained even with topographic constraints ( $\tau$ ), we evaluated the predictive abilities of TopoAudios and the baseline ResNet50 architecture using two fMRI datasets, NH2015 (Norman-Haignere et al., 2015) and B2021 (Boebinger et al., 2021). Following prior work (Tuckute et al., 2023), we computed the voxel-wise explained variance (adjusted  $R^2$ ) using linear regression across each layer of the model hierarchy.

Figure 2 shows that both baseline and TopoAudios achieved comparable levels of predictivity across layers. This is evident in the qualitative prediction maps projected onto the cortical surface (Figure 2A), where both models showed similar levels of adjusted  $R^2$  across voxels. Both models also showed characteristic features of cortical predictivity. Prediction accuracies improve across model layers. This is apparent more clearly in Figure 2B which shows that model prediction accuracy peaks around the 6th topographic layer. It is particularly striking that prediction accuracy is nearly indistinguishable between the baseline and TopoAudios. The five curves corresponding to the baseline model and the different topographic variants of TopoAudios are virtually superimposed. As a further quantification, Figure 2C demonstrates that adding the topographic constraint does little to reduce the overall model prediction accuracy in both the ResNet50 architecture and the AST archi-



394  
395  
396  
397

**Figure 4: TopoAudio models show late auditory representations related to speech and music selectivity.** Selectivity maps show  $t$ -values for speech (green) and music (blue) preferences, with baseline models (top row) lacking the clear modular structure seen in the TopoAudio models (bottom row).

400  
401  
402  
403  
404  
405  
406  
407  
408  
409  
410  
411  
412  
413  
414  
415  
416  
417  
418  
419  
420  
421  
422  
423  
424  
425  
426  
427  
428  
429  
430  
431

ture. This pattern held not only across the whole auditory cortex but also within specific regions of interest (ROIs obtained from (Norman-Haiglere et al., 2015)). When we repeated the analysis separately for early tonotopic regions, pitch-selective regions, and higher-order music and speech areas, we observed the same trends. TopoAudios were as predictive as baseline models for all ROIs. Together these results confirm that inducing topographic constraints do not impair their ability to predict fMRI responses in auditory cortex. Thus, TopoAudios preserve both task performance (on engineering metrics) and predictive accuracy (on 2 distinct fMRI datasets) while producing spatially structured internal representations. The similarity of the TopoAudios to the baseline models leads to a natural question: **are these models actually the same, or are our evaluations not sensitive enough to reveal the differences?**

#### 4.3 TOPONETS RECAPITULATE THE SIGNATURES OF EARLY AND LATE AUDITORY PROCESSING IN THE BRAIN

To evaluate whether TopoAudios develop biologically meaningful auditory representations, we examined whether these models show known signatures of auditory processing. Specifically, we assessed whether the topographic structures within the TopoAudios give rise to tonotopic and amplitude modulation (AM) maps, typically considered features of early auditory processing, as well as selective responses to music and speech, characteristic of higher-order auditory areas.

Figure 3A shows the observed tonotopic maps in the early layers (layer 1.1 and layer 2.1 in ResNet50s and blocks.9.mlp.fc1 in ASTs) of the baseline and topographic models. The frequency preferences appear randomly distributed on the cortical sheet for the baseline models (top). In contrast, the same layers for the TopoAudio model (below) show a smooth frequency gradients which qualitatively resembles the tonotopic organization observed in primary auditory cortex. Similarly, in the AM tuning maps (Figure 3B), the baseline model is fragmented and disorganized, while the TopoAudio model develops smooth spatial transitions, considered another hallmark of early auditory areas.

Figure 4 examines the late-stage selectivity for speech and music observed in the human auditory cortex using fMRI-like selectivity maps (see section 3) applied to a later layer (layer 3.1 in ResNet50 and blocks.9.mlp.fc1 in ASTs) of baseline and TopoAudio models. For both speech (green) and music (blue), baseline models (top row) show spatially inconsistent selectivity on the cortical sheet. By contrast, TopoAudios exhibit spatially clustered patches of selectivity for speech and music, mirroring the modular organization observed in non-primary auditory cortex. This result is striking, as such modularity for music and speech emerged purely from task optimization with spatial con-

432  
 433  
 434  
 435  
 436  
 437  
 438  
 439  
 440  
 441  
 442  
 443  
 444  
 445  
 446  
 447  
 448  
 449  
 450  
 451  
 452  
 453  
 454  
 455  
 456  
 457  
 458  
 459  
 460  
 461  
 462  
 463  
 464  
 465  
 466  
 467  
 468  
 469  
 470  
 471  
 472  
 473  
 474  
 475  
 476  
 477  
 478  
 479  
 480  
 481  
 482  
 483  
 484  
 485

**How similar are the speech and music ICA components from the brain to the ICA components from TopoAudio?**

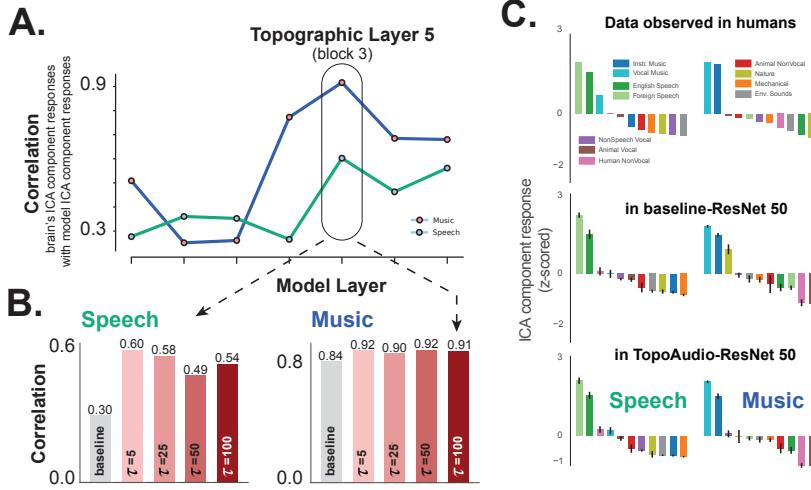


Figure 5: **TopoAudio models better align with human speech and music-selective cortical components.** (A) Correlation between model-derived ICA components and brain-inferred ICA components selective for speech (green) and music (blue), across layers of the ResNet50 hierarchy. TopoAudios show the highest similarity with brain components at layer 3, consistent with the emergence of high-level selectivity in the auditory cortex. (B) Summary of brain-model ICA component correlations for each TopoNet variant ( $\tau = 5-100$ ) compared to the baseline ResNet50. Topographic models yield higher median correlation with brain-derived components for both music and speech. (C) Category response profiles of ICA components derived from human fMRI (top), baseline ResNet50 (middle), and TopoAudio (bottom). Responses are grouped by stimulus categories.

straints. However, a limitation of this finding is its qualitative nature. To address this concern, we next quantified the correspondence between model-based selectivity maps and empirical fMRI data from human auditory cortex

Using human fMRI responses to a large set of natural sounds, selectivity for music and speech is often inferred by factorizing the fMRI responses from the auditory cortex into spatial components using ICA. This approach consistently reveals components that are selectively responsive to music or speech stimuli (Norman-Haignere et al., 2015; Boebinger et al., 2021). To evaluate whether such category-selective structure emerges in our models, we applied the same analysis to the activation patterns in TopoAudios. For each model layer, we performed the non-parametric decomposition algorithm (Norman-Haignere et al., 2015) on the model unit responses (using six components, consistent with human analyses) and identified the component that best matched the brain-inferred music or speech component. In Figure 5A, we show the correlation between brain and model components across the model hierarchy. For both music and speech, TopoAudios showed the highest correlation with the fMRI components at layer 3, mirroring the depth at which late-stage selectivity emerges in the human auditory cortex.

We next quantified these correlations across all model variants. As shown in Figure 5B, the TopoAudios consistently produced higher correlations with brain-inferred components than the baseline models. For the music component, the median correlation across TopoAudio variants was 0.915, compared to 0.84 for the baseline. For the speech component, the TopoAudio models again showed higher median correlation (0.56) compared to the baseline (0.30). These results indicate that topographic constraints enhance the emergence of music- and speech-selective representations that align more closely with those observed in the human brain. We then plotted the response profiles of the components derived from humans, the baseline model, and the TopoAudio models grouped by the auditory stimulus categories from the original dataset (Norman-Haignere et al., 2015) in Figure 5C. The inferred components from the brain (top), the baseline model (middle) and the TopoAudios exhibited clear and selective responses to music and speech categories, confirming that the model components capture aspects of music and speech selectivity also observed in human brains.

## 486 5 DISCUSSION

488 In this work, we tested whether the topographic organization of the auditory cortex could emerge in  
 489 deep neural networks by optimizing for auditory tasks under a spatial smoothness constraint. We in-  
 490 troduced TopoAudio, the first end-to-end topographic models of the auditory system. These models  
 491 recapitulate the hierarchical organization of auditory cortex and reproduce hallmark features such as  
 492 smooth tonotopic and amplitude-modulation maps in early layers, and spatially clustered selectiv-  
 493 ity for music and speech in later layers, all while maintaining strong auditory task performance and  
 494 fMRI predictivity. None of these features were hand-engineered. They emerged naturally from task-  
 495 driven optimization combined with a topographic constraint. Crucially, the topographic models also  
 496 provide a closer match to the internal structure of auditory cortex. Compared to non-topographic  
 497 baselines, TopoAudio models align significantly better with ICA maps derived from human fMRI  
 498 data. This suggests that our models not only predict the brain’s responses but also better capture the  
 499 fine-grained representational geometry that underlies how the brain organizes sound. In doing so,  
 500 they offer a stronger test of model–brain similarity, moving beyond surface-level prediction toward  
 501 an assessment of deeper structural and computational alignment.

502 Our findings in audition, combined with prior topographic modeling work in vision and language,  
 503 provide strong corroborating evidence for a unified computational strategy employed by the brain  
 504 to efficiently encode information under its architectural constraints. This success in a new sensory  
 505 domain provides a powerful test of the principle’s generality, showing it is not a quirk of visual  
 506 processing but a foundational component of sensory representation across the cortex. Further, the  
 507 similarity of topographic structure between models and biological systems can serve as an additional  
 508 evaluation of models in an era where many models seem to be performing equally well on many of  
 509 our standard benchmarks (Tuckute et al., 2023; Conwell et al., 2024; Ratan Murty et al., 2021;  
 Feather et al., 2025).

510 The primary focus of this work was to evaluate whether our topographic auditory models capture the  
 511 representational features observed in biological auditory systems. It is important to note that there  
 512 is a long history in auditory neuroscience of searching for auditory maps. Multiple studies have  
 513 suggested that the topographic structure of auditory cortex might in fact be quite complex (Schreiner  
 514 & Winer, 2007; Kanold et al., 2014; Middlebrooks, 2021), and that we do not yet have a good  
 515 description of its organization. **For example, even though there is general agreement that speech**  
 516 **and music selective neural populations exist in the brain, the general locations and numbers of such**  
 517 **patches are not well characterized.** Future data collected to characterize the biological topography  
 518 **of the auditory system can be incorporated into evaluations of topographic models.** Additionally, by  
 519 building topographic models of auditory cortex trained on natural stimuli, TopoAudios can serve as  
 520 a computational tool for exploring and testing theories of cortical organization, potentially revealing  
 521 previously unknown structure in auditory cortex.

522 **Limitations and Future work:** This work serves as a starting point for topographic auditory mod-  
 523 els. Here, we only investigated two DNN architectures trained on the same task, but the same type  
 524 of topographic loss could be applied to other DNN architectures or combined with a different set of  
 525 tasks. Additionally, other datasets may be better for evaluating details of the topographic structure  
 526 of the auditory system, as the fMRI dataset lacks fine-grained temporal resolution and may hide  
 527 some spatial structure Norman-Haignere et al. (2022). Nevertheless, the present results provide a  
 528 computational framework for studying the emergence of cortical organization toward models that  
 529 unify task performance with biological structure.

530  
 531  
 532  
 533  
 534  
 535  
 536  
 537  
 538  
 539

540 REFERENCES  
541

542 Emily J Allen, Juraj Mesik, Kendrick N Kay, and Andrew J Oxenham. Distinct representations of  
543 tonotopy and pitch in human auditory cortex. *Journal of Neuroscience*, 42(3):416–434, 2022.

544 Simon Baumann, Timothy D Griffiths, Li Sun, Christopher I Petkov, Alexander Thiele, and Adrian  
545 Rees. Orthogonal representation of sound dimensions in the primate midbrain. *Nature neuro-  
546 science*, 14(4):423–425, 2011.

547 Simon Baumann, Olivier Joly, Adrian Rees, Christopher I Petkov, Li Sun, Alexander Thiele, and  
548 Timothy D Griffiths. The topography of frequency and time representation in primate auditory  
549 cortices. *elife*, 4:e03256, 2015.

550 Daniel Bendor and Xiaoqin Wang. The neuronal representation of pitch in primate auditory cortex.  
551 *Nature*, 436(7054):1161–1165, 2005.

552 Taha Binhuraib, Greta Tuckute, and Nicholas Blauch. Topoformer: brain-like topographic organi-  
553 zation in transformer language models through spatial querying and reweighting. *arXiv preprint  
554 arXiv:2510.18745*, 2025.

555 Gary G Blasdel. Orientation selectivity, preference, and continuity in monkey striate cortex. *Journal  
556 of Neuroscience*, 12(8):3139–3161, 1992.

557 Dana Boebinger, Sam V Norman-Haignere, Josh H McDermott, and Nancy Kanwisher. Music-  
558 selective neural populations arise without musical training. *Journal of Neurophysiology*, 125(6):  
559 2237–2263, 2021.

560 Alyssa A Brewer and Brian Barton. Maps of the auditory cortex. *Annual review of neuroscience*, 39  
561 (1):385–407, 2016.

562 Dmitri B Chklovskii and Alexei A Koulakov. Maps in the brain: what can we learn from them?  
563 *Annu. Rev. Neurosci.*, 27(1):369–392, 2004.

564 Colin Conwell, Jacob S Prince, Kendrick N Kay, George A Alvarez, and Talia Konkle. A large-scale  
565 examination of inductive biases shaping high-level visual representation in brains and machines.  
566 *Nature communications*, 15(1):9383, 2024.

567 Peter Dallos, Arthur N Popper, and Richard R Fay. The cochlea. 1996.

568 Mayukh Deb, Mainak Deb, and Apurva Ratan Murty. Toponets: High performing vision and lan-  
569 guage models with brain-like topography. In *The Thirteenth International Conference on Learn-  
570 ing Representations*, 2025. URL <https://openreview.net/forum?id=THqWPzL00e>.

571 Amirozhan Dehghani, Xinyu Qian, Asa Farahani, and Pouya Bashivan. Credit-based self organiz-  
572 ing maps: training deep topographic networks with minimal performance degradation. In *The  
573 Thirteenth International Conference on Learning Representations*, 2024.

574 Paul E Downing, Yuhong Jiang, Miles Shuman, and Nancy Kanwisher. A cortical area selective for  
575 visual processing of the human body. *Science*, 293(5539):2470–2473, 2001.

576 Paul E Downing, AW-Y Chan, Marius Vincent Peelen, CM Dodds, and N Kanwisher. Domain  
577 specificity in visual cortex. *Cerebral cortex*, 16(10):1453–1461, 2006.

578 Jesse Engel, Cinjon Resnick, Adam Roberts, Sander Dieleman, Douglas Eck, Karen Simonyan, and  
579 Mohammad Norouzi. Neural Audio Synthesis of Musical Notes with WaveNet Autoencoders,  
580 April 2017. URL <http://arxiv.org/abs/1704.01279>. arXiv:1704.01279 [cs].

581 Russell Epstein, Alison Harris, Damian Stanley, and Nancy Kanwisher. The parahippocampal place  
582 area: recognition, navigation, or encoding? *Neuron*, 23(1):115–125, 1999.

583 Jenelle Feather, Alex Durango, Ray Gonzalez, and Josh McDermott. Metamers of neural networks  
584 reveal divergence from human perceptual systems. *Advances in Neural Information Processing  
585 Systems*, 32, 2019.

594 Jenelle Feather, Meenakshi Khosla, N Murty, and Aran Nayebi. Brain-model evaluations need the  
 595 neuroai turing test. *arXiv preprint arXiv:2502.16238*, 2025.

596

597 Evelina Fedorenko, Josh H McDermott, Sam Norman-Haignere, and Nancy Kanwisher. Sensitivity  
 598 to musical structure in the human brain. *Journal of neurophysiology*, 108(12):3289–3300, 2012.

599 Andrew Frnci and Josh H McDermott. Deep neural network models of sound localization reveal  
 600 how perception is adapted to real-world environments. *Nature human behaviour*, 6(1):111–133,  
 601 2022.

602

603 Bruno L Giordano, Michele Esposito, Giancarlo Valente, and Elia Formisano. Intermediate acoustic-  
 604 to-semantic representations link behavioral and neural responses to natural sounds. *Nature Neu-  
 605 roscience*, 26(4):664–672, 2023.

606 Brian R Glasberg and Brian CJ Moore. Derivation of auditory filter shapes from notched-noise data.  
 607 *Hearing research*, 47(1-2):103–138, 1990.

608

609 Yuan Gong, Yu-An Chung, and James Glass. Ast: Audio spectrogram transformer, 2021. URL  
 610 <https://arxiv.org/abs/2104.01778>.

611

612 Kalanit Grill-Spector, Nicholas Knouf, and Nancy Kanwisher. The fusiform face area subserves  
 613 face perception, not generic within-category identification. *Nature neuroscience*, 7(5):555–562,  
 2004.

614

615 Umut Güçlü, Jordy Thielen, Michael Hanke, and Marcel Van Gerven. Brains on beats. *Advances in  
 616 Neural Information Processing Systems*, 29, 2016.

617

618 Ilana Harris, Efe C Niven, Alex Griffin, and Sophie K Scott. Is song processing distinct and special  
 619 in the auditory cortex? *Nature Reviews Neuroscience*, 24(11):711–722, 2023.

620

621 Kaiming He, Xiangyu Zhang, Shaoqing Ren, and Jian Sun. Deep Residual Learning for  
 622 Image Recognition, December 2015. URL <http://arxiv.org/abs/1512.03385>.  
 arXiv:1512.03385 [cs].

623

624 Robert A Jacobs and Michael I Jordan. Computational consequences of a bias toward short connec-  
 625 tions. *Journal of cognitive neuroscience*, 4(4):323–336, 1992.

626

627 Philip X Joris, Christoph E Schreiner, and Adrian Rees. Neural processing of amplitude-modulated  
 628 sounds. *Physiological reviews*, 84(2):541–577, 2004.

629

630 Jon H Kaas. Topographic maps are fundamental to sensory processing. *Brain Re-  
 631 search Bulletin*, 44(2):107–112, 1997. ISSN 0361-9230. doi: [https://doi.org/10.1016/S0361-9230\(97\)00094-4](https://doi.org/10.1016/S0361-9230(97)00094-4). URL <https://www.sciencedirect.com/science/article/pii/S0361923097000944>.

632

633 Patrick O Kanold, Israel Nelken, and Daniel B Polley. Local versus global scales of organization in  
 634 auditory cortex. *Trends in neurosciences*, 37(9):502–510, 2014.

635

636 Nancy Kanwisher. Domain specificity in face perception. *Nature neuroscience*, 3(8):759–763, 2000.

637

638 Alexander JE Kell, Daniel LK Yamins, Erica N Shook, Sam V Norman-Haignere, and Josh H Mc-  
 639 Dermott. A task-optimized neural network replicates human auditory behavior, predicts brain  
 640 responses, and reveals a cortical processing hierarchy. *Neuron*, 98(3):630–644, 2018.

641

642 Fatemeh Khatami and Monty A Escabí. Spiking network optimized for word recognition in noise  
 643 predicts auditory system hierarchy. *PLOS Computational Biology*, 16(6):e1007558, 2020.

644

645 Eric I Knudsen and Masakazu Konishi. A neural map of auditory space in the owl. *Science*, 200  
 646 (4343):795–797, 1978.

647

648 Talia Konkle and Alfonso Caramazza. Tripartite organization of the ventral stream by animacy and  
 649 object size. *Journal of Neuroscience*, 33(25):10235–10242, 2013.

650

651 Talia Konkle and Aude Oliva. Canonical visual size for real-world objects. *Journal of Experimental  
 652 Psychology: human perception and performance*, 37(1):23, 2011.

648   Takuya Koumura, Hiroki Terashima, and Shigeto Furukawa. Human-like modulation sensitivity  
 649   emerging through optimization to natural sound recognition. *Journal of Neuroscience*, 43(21):  
 650   3876–3894, 2023.

651   Amber M Leaver and Josef P Rauschecker. Cortical representation of natural complex sounds:  
 652   effects of acoustic features and auditory object category. *Journal of neuroscience*, 30(22):7604–  
 653   7612, 2010.

654   Amber M Leaver and Josef P Rauschecker. Functional topography of human auditory cortex. *Jour-  
 655   nal of Neuroscience*, 36(4):1416–1428, 2016.

656   Hyodong Lee, Eshed Margalit, Kamila M Jozwik, Michael A Cohen, Nancy Kanwisher, Daniel LK  
 657   Yamins, and James J DiCarlo. Topographic deep artificial neural networks reproduce the hall-  
 658   marks of the primate inferior temporal cortex face processing network. *BioRxiv*, pp. 2020–07,  
 659   2020.

660   Eshed Margalit, Hyodong Lee, Dawn Finzi, James J. DiCarlo, Kalanit Grill-Spector, and Daniel  
 661   L. K. Yamins. A unifying framework for functional organization in early and higher ventral visual  
 662   cortex. *Neuron*, 112(14):2435–2451.e7, July 2024. ISSN 0896-6273. doi: 10.1016/j.neuron.  
 663   2024.04.018. URL [https://www.cell.com/neuron/abstract/S0896-6273\(24\)00279-4](https://www.cell.com/neuron/abstract/S0896-6273(24)00279-4). Publisher: Elsevier.

664   Bruce D McCandliss, Laurent Cohen, and Stanislas Dehaene. The visual word form area: expertise  
 665   for reading in the fusiform gyrus. *Trends in cognitive sciences*, 7(7):293–299, 2003.

666   Josh H McDermott and Eero P Simoncelli. Sound texture perception via statistics of the auditory  
 667   periphery: evidence from sound synthesis. *Neuron*, 71(5):926–940, 2011.

668   Paul Mermelstein. Distance measures for speech recognition, psychological and instrumental. *Pat-  
 669   tern recognition and artificial intelligence*, 116:374–388, 1976.

670   John C Middlebrooks. A search for a cortical map of auditory space. *Journal of Neuroscience*, 41  
 671   (27):5772–5778, 2021.

672   Juliette Millet, Charlotte Caucheteux, Yves Boubenec, Alexandre Gramfort, Ewan Dunbar,  
 673   Christophe Pallier, Jean-Remi King, et al. Toward a realistic model of speech processing in  
 674   the brain with self-supervised learning. *Advances in Neural Information Processing Systems*, 35:  
 675   33428–33443, 2022.

676   M Moerel, F De Martino, and E Formisano. An anatomical and functional topography of human  
 677   auditory cortical areas. *front neurosci*. 2014; 8: 225, 2014.

678   Sam Norman-Haignere, Nancy Kanwisher, and Josh H McDermott. Cortical pitch regions in humans  
 679   respond primarily to resolved harmonics and are located in specific tonotopic regions of anterior  
 680   auditory cortex. *Journal of Neuroscience*, 33(50):19451–19469, 2013.

681   Sam Norman-Haignere, Nancy G Kanwisher, and Josh H McDermott. Distinct cortical pathways for  
 682   music and speech revealed by hypothesis-free voxel decomposition. *neuron*, 88(6):1281–1296,  
 683   2015.

684   Sam V Norman-Haignere, Jenelle Feather, Dana Boebinger, Peter Brunner, Anthony Ritaccio,  
 685   Josh H McDermott, Gerwin Schalk, and Nancy Kanwisher. A neural population selective for  
 686   song in human auditory cortex. *Current Biology*, 32(7):1470–1484, 2022.

687   Christo Pantev, Olivier Bertrand, Carsten Eulitz, Chantal Verkindt, S Hampson, Gerhard Schuierer,  
 688   and Thomas Elbert. Specific tonotopic organizations of different areas of the human auditory  
 689   cortex revealed by simultaneous magnetic and electric recordings. *Electroencephalography and  
 690   clinical neurophysiology*, 94(1):26–40, 1995.

691   Karol J. Piczak. ESC: Dataset for Environmental Sound Classification. In *Proceedings of the 23rd  
 692   ACM international conference on Multimedia*, MM '15, pp. 1015–1018, New York, NY, USA,  
 693   October 2015. Association for Computing Machinery. ISBN 978-1-4503-3459-4. doi: 10.1145/  
 694   2733373.2806390. URL <https://dl.acm.org/doi/10.1145/2733373.2806390>.

702 Xinyu Qian, Amir Ozhan Dehghani, Asa Borzabadi Farahani, and Pouya Bashivan. Local lateral  
 703 connectivity is sufficient for replicating cortex-like topographical organization in deep neural net-  
 704 works. *bioRxiv*, pp. 2024–08, 2024.

705

706 N Apurva Ratan Murty, Pouya Bashivan, Alex Abate, James J DiCarlo, and Nancy Kanwisher. Com-  
 707 putational models of category-selective brain regions enable high-throughput tests of selectivity.  
 708 *Nature communications*, 12(1):5540, 2021.

709

710 Neil Rathi, Johannes Mehrer, Badr AlKhamissi, Taha Binhuraib, Nicholas M Blauch, and Martin  
 711 Schrimpf. Topolm: brain-like spatio-functional organization in a topographic language model.  
 712 *arXiv preprint arXiv:2410.11516*, 2024.

713

714 Neil Rathi, Johannes Mehrer, Badr AlKhamissi, Taha Binhuraib, Nicholas M. Blauch, and Martin  
 715 Schrimpf. Topolm: brain-like spatio-functional organization in a topographic language model,  
 716 2025. URL <https://arxiv.org/abs/2410.11516>.

717

718 Heather L Read, Jeffery A Winer, and Christoph E Schreiner. Functional architecture of auditory  
 719 cortex. *Current opinion in neurobiology*, 12(4):433–440, 2002.

720

721 Richard A Reale and Thomas J Imig. Tonotopic organization in auditory cortex of the cat. *Journal  
 722 of Comparative Neurology*, 192(2):265–291, 1980.

723

724 Kyle M Rupp, Jasmine L Hect, Emily E Harford, Lori L Holt, Avniel Singh Ghuman, and Taylor J  
 725 Abel. A hierarchy of processing complexity and timescales for natural sounds in the human  
 726 auditory cortex. *Proceedings of the National Academy of Sciences*, 122(18):e2412243122, 2025.

727

728 Mark R Saddler and Josh H McDermott. Models optimized for real-world tasks reveal the task-  
 729 dependent necessity of precise temporal coding in hearing. *Nature Communications*, 15(1):1–29,  
 730 2024.

731

732 Mark R Saddler, Andrew Franci, Jenelle Feather, Kaizhi Qian, Yang Zhang, and Josh H McDermott.  
 733 Speech denoising with auditory models. *arXiv preprint arXiv:2011.10706*, 2020.

734

735 Mark R Saddler, Ray Gonzalez, and Josh H McDermott. Deep neural network models reveal inter-  
 736 play of peripheral coding and stimulus statistics in pitch perception. *Nature communications*, 12  
 737 (1):7278, 2021.

738

739 Henning Scheich. Auditory cortex: comparative aspects of maps and plasticity. *Current opinion in  
 740 neurobiology*, 1(2):236–247, 1991.

741

742 Christoph E Schreiner and Jeffery A Winer. Auditory cortex mapmaking: principles, projections,  
 743 and plasticity. *Neuron*, 56(2):356–365, 2007.

744

745 Malcolm Slaney. Auditory toolbox. *Interval Research Corporation, Tech. Rep*, 10(1998):1194,  
 746 1998.

747

748 Greta Tuckute, Jenelle Feather, Dana Boebinger, and Josh H. McDermott. Many but not all  
 749 deep neural network audio models capture brain responses and exhibit correspondence between  
 750 model stages and brain regions. *PLOS Biology*, 21(12):e3002366, December 2023. ISSN  
 751 1545-7885. doi: 10.1371/journal.pbio.3002366. URL <https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.3002366>. Publisher: Public  
 752 Library of Science.

753

754 Aditya R Vaidya, Shailee Jain, and Alexander G Huth. Self-supervised models of audio effectively  
 755 explain human cortical responses to speech. *arXiv preprint arXiv:2205.14252*, 2022.

756

757 Pete Warden. Speech commands: A dataset for limited-vocabulary speech recognition, 2018. URL  
 758 <https://arxiv.org/abs/1804.03209>.

759

760 C Mark Wessinger, Michael H Buonocore, Clif L Kussmaul, and George R Mangun. Tonotopy  
 761 in human auditory cortex examined with functional magnetic resonance imaging. *Human brain  
 762 mapping*, 5(1):18–25, 1997.

756 Jamal A Williams, Elizabeth H Margulis, Samuel A Nastase, Janice Chen, Uri Hasson, Kenneth A  
757 Norman, and Christopher Baldassano. High-order areas and auditory cortex both represent the  
758 high-level event structure of music. *Journal of cognitive neuroscience*, 34(4):699–714, 2022.  
759

760 Robert J Zatorre, Pascal Belin, and Virginia B Penhune. Structure and function of auditory cortex:  
761 music and speech. *Trends in cognitive sciences*, 6(1):37–46, 2002.  
762  
763  
764  
765  
766  
767  
768  
769  
770  
771  
772  
773  
774  
775  
776  
777  
778  
779  
780  
781  
782  
783  
784  
785  
786  
787  
788  
789  
790  
791  
792  
793  
794  
795  
796  
797  
798  
799  
800  
801  
802  
803  
804  
805  
806  
807  
808  
809

810 A APPENDIX  
811812 A.1 TOPOAUDIO PERFORMANCE  
813

814 Table 1 reports classification accuracy and representational smoothness for both baseline and topo-  
815 graphic variants of Transformer-B/32 and ResNet-50 backbones. Across datasets (ESC50, NSynth,  
816 and Speech Commands), accuracy remains nearly unchanged when introducing topographic con-  
817 straints ( $\tau$ ), with performance differences typically within  $< 1\%$  of baseline. In contrast, smooth-  
818 ness values increase substantially, confirming that topographic regularization induces more spatially  
819 coherent representations. These results demonstrate that TopoAudio models preserve strong classifi-  
820 cation performance while simultaneously improving internal topographic structure, supporting their  
821 utility as both effective and interpretable auditory models.

822  
823 Table 1: **Topographic auditory models maintain high classification performance across**  
824 **evaluations.** Accuracy is reported for ESC50, NSynth, and Speech Command datasets using  
825 Transformer-B/32 and ResNet-50 backbones. While baseline models achieve slightly higher accu-  
826 racy, introducing topographic constraints ( $\tau$ ) substantially increases representational smoothness  
827 with only modest changes in classification performance. Topographic Avg. indicates the mean  
828 performance across all non-baseline  $\tau$  values.

830 <b>Topography (<math>\tau</math>)</b>	831 <b>Accuracy</b>			832 <b>Smoothness</b>
	833 ESC50	NSynth	SpeechCmd	
<b>834 Transformer-B/32</b>				
835 Baseline	82.10	98.25	92.94	0.31
836 5	81.94	98.13	92.63	0.46
838 25	82.01	98.13	92.80	0.50
839 50	81.66	97.99	92.42	0.57
840 100	81.88	97.91	92.38	0.56
841 <i>Topographic Avg.</i>	81.87	98.04	92.56	0.52
<b>843 ResNet-50</b>				
845 Baseline	81.69	98.29	86.68	0.34
846 5	81.46	98.50	86.88	1.10
847 25	80.62	98.39	87.89	0.87
848 50	80.84	98.36	87.57	1.04
849 100	80.32	98.72	86.85	1.09
850 200	80.70	98.48	87.47	0.93
852 <i>Topographic Avg.</i>	80.79	98.49	87.33	1.01

## 855 B COMPUTATION OF MORAN'S I SPATIAL AUTOCORRELATION

856 Moran's I is a metric of global spatial autocorrelation that quantifies the degree to which values  
857 defined over a spatial domain exhibit smooth clustering or random dispersion (Rathi et al., 2024).  
858 Formally, for a set of values  $x_i$  arranged over  $N$  spatial units, Moran's I is defined as:  
859

$$860 I = \frac{N}{W} \frac{\sum_i \sum_j w_{ij} (x_i - \bar{x})(x_j - \bar{x})}{\sum_i (x_i - \bar{x})^2}, \quad (7)$$

864 where  $\bar{x}$  is the global mean,  $w_{ij}$  are entries of a sparse adjacency matrix encoding the neighborhood  
 865 relationships among vertices or units, and  $W = \sum_{i,j} w_{ij}$  is the total connection weight. Values of  
 866 Moran’s I range from  $-1$  to  $1$ , with positive values reflecting spatially smooth and contiguous organization,  
 867 values near zero indicating spatial randomness, and negative values indicating systematic  
 868 spatial dispersion.

869

870

### 871 B.1 MORAN’S I FOR BRAIN MAPS

872

873 To compute Moran’s I for human auditory cortex, we generated several cortical maps derived from  
 874 fMRI responses, including music-selective and speech-selective contrast maps. We constructed a  
 875 binary vertex adjacency matrix in which each vertex is connected to its immediate geometric neighbors  
 876 in the surface tessellation (typically six per vertex). Prior to computing Moran’s I, vertices  
 877 failing to meet a statistical significance threshold (e.g., FDR-corrected  $p < 0.05$ ) were zero-masked  
 878 to remove noise-driven fluctuations. Moran’s I was then evaluated directly on these spatial contrast  
 879 maps, yielding a quantitative estimate of the smoothness of the underlying functional organization  
 880 on category-selective gradients.

881

882

### 883 B.2 MORAN’S I FOR COMPUTATIONAL MODELS

884

885

886 For neural network models, we applied an analogous spatial autocorrelation procedure by imposing  
 887 a fixed two-dimensional topographic layout over the units of each layer. Specifically, units within  
 888 each MLP block (or convolutional feature map) were assigned to positions on a 2D grid, and a binary  
 889 adjacency matrix was constructed based on local grid connectivity. Using this spatial structure, we  
 890 computed selectivity maps for each model, including frequency tonotopy maps, modulation-rate  
 891 maps, and music- vs.-other and speech- vs.-other contrast maps derived from model activations.  
 892 Moran’s I was computed for each layer individually and then averaged across relevant layers to  
 893 obtain a model-level smoothness estimate for each topographic strength  $\tau$ . This procedure mirrors  
 894 the approach used for fMRI maps, enabling direct comparison between cortical organization and  
 895 the representational smoothness learned by neural networks trained with and without topographic  
 896 constraints.

897

898

### 899 B.3 MORAN’S I RESULTS

900

901

902 Table 2 summarizes the Moran’s I values for the two model classes considered—ResNet-50 and  
 903 AST-Base—across varying topographic strengths  $\tau$ . Several clear patterns emerge from this com-  
 904 parison. First, the baseline condition ( $\tau = 0$ ) produces Moran’s I values at or near zero across  
 905 all four map types (tonotopy, amplitude modulation, music, and speech), confirming that without  
 906 explicit spatial regularization neither architecture develops meaningful topographic structure. This  
 907 reinforces that standard convolutional or transformer-based audio models do not spontaneously ac-  
 908 quire spatial contiguity in their feature maps.

909

910

911 Introducing topographic regularization ( $\tau > 0$ ), however, yields large and systematic increases in  
 912 spatial autocorrelation for both architectures. In AST-Base, smoothness increases consistently from  
 913  $\tau = 5$  to  $\tau = 50$ , with only a slight saturation at  $\tau = 100$ , indicating that moderate levels of  
 914 spatial pressure are sufficient to induce stable and biologically interpretable organization. Similar  
 915 improvements appear in ResNet-50, where  $\tau = 50$  and  $\tau = 100$  produce substantial topographic  
 916 structure across all selectivity types. Notably, music- and speech-selective maps in ResNet-50 reach  
 917 Moran’s I values in the  $0.80$ – $0.83$  range, approaching the upper-bound smoothness observed in  
 918 human auditory cortex.

919

920

921 Finally, the brain exhibits near-ceiling spatial autocorrelation (0.99 for both music and speech),  
 922 serving as a reference for the maximum smoothness achievable in biological systems. The fact  
 923 that topographically constrained models—particularly at higher  $\tau$  levels—approach these values  
 924 demonstrates that imposing spatial continuity enables artificial networks to replicate key hallmarks  
 925 of cortical organization. This alignment between model- and brain-derived maps highlights the util-  
 926 ity of topographic constraints as a principled mechanism for shaping neural network representations  
 927 toward neurobiological structure.

918  
 919 **Table 2: Topographic smoothness of music-, speech-, tonotopic-, and AM-selective maps.**  
 920 Moran’s I spatial autocorrelation for ResNet-50, AST-Base, and human brain fMRI.

921 <b>Selectivity</b>	922 <b>ResNet-50</b>					923 <b>AST-Base</b>					924 <b>Brain</b> (NH2015)
	925 $\tau=0$	926 $\tau=5$	927 $\tau=25$	928 $\tau=50$	929 $\tau=100$	930 $\tau=0$	931 $\tau=5$	932 $\tau=25$	933 $\tau=50$	934 $\tau=100$	
<b>Tonotopy</b>	-0.01	0.54	0.59	0.67	0.67	0.00	0.43	0.50	0.52	0.49	–
<b>Amplitude Modulation</b>	-0.01	0.55	0.56	0.34	0.46	0.00	0.33	0.38	0.45	0.44	–
<b>Music</b>	0.01	0.79	0.78	0.83	0.80	0.00	0.62	0.71	0.73	0.73	0.99
<b>Speech</b>	-0.01	0.75	0.78	0.79	0.82	0.00	0.61	0.69	0.71	0.72	0.99

## 926 **C FMRI DATASETS**

### 927 **C.1 NH2015**

928 The fMRI data used in this study are a subset of those originally reported in (Norman-Haignere  
 929 et al., 2015), with procedures summarized below.

930 **Participants and Experimental Design.** Eight right-handed, native English-speaking participants  
 931 (4 female; mean age 22 years, range 19–25) with normal hearing and no formal musical training  
 932 participated in the study. Each participant completed three fMRI sessions (~2 hours each). Five  
 933 additional participants were excluded due to either incomplete scanning sessions or excessive head  
 934 motion and task non-compliance. All participants gave informed consent under protocols approved  
 935 by the MIT Committee on the Use of Humans as Experimental Subjects (protocol 2105000382).

936 **Stimuli.** A total of 165 two-second natural sounds were selected to span a wide range of real-world  
 937 auditory categories. Each sound was validated using a 10-way forced-choice classification task on  
 938 Amazon Mechanical Turk and included only if recognized with at least 80% accuracy. Stimulus  
 939 names and categories are available in the supplementary materials of (Tuckute et al., 2023), and the  
 940 full stimulus set can be downloaded from: <http://mcdermottlab.mit.edu/downloads.html>.

941 **fMRI Procedure.** Stimuli were presented in a blocked design, with each block consisting of five  
 942 repetitions of the same 2-second sound, interleaved with 200 ms of silence to minimize scanner  
 943 noise. Each block lasted 17 s (TR = 3.4 s), and silence blocks of equal duration were interspersed  
 944 to estimate baseline responses. To ensure attentiveness, participants performed an intensity discrim-  
 945 ination task in each block, identifying the quietest sound (7 dB lower than the others) via button  
 946 press.

947 **Data Acquisition.** Data were acquired on a 3T Siemens Trio scanner with a 32-channel head coil  
 948 at the Athinoula A. Martinos Imaging Center (MIT). Each run consisted of 15 slices oriented parallel  
 949 to the superior temporal plane (TR = 3.4 s, TE = 30 ms, flip angle = 90°). The in-plane resolution  
 950 was 2.1 mm × 2.1 mm, with 4 mm thick slices and a 10% gap (voxel size: 2.1 × 2.1 × 4.4 mm).  
 951 The first 5 volumes of each run were discarded.

952 **Preprocessing.** Preprocessing was conducted using FSL, FreeSurfer, and custom MATLAB  
 953 scripts. Functional data were motion- and slice-time corrected, linearly detrended, skull-stripped,  
 954 and aligned to each participant’s anatomical scan using FLIRT and BBRegister. Volumes were pro-  
 955 jected to the reconstructed cortical surface using FreeSurfer and smoothed with a 3-mm FWHM  
 956 2D Gaussian kernel. Percent signal change was computed relative to silence blocks, and responses  
 957 were downsampled to a 2-mm isotropic grid on the FreeSurfer surface. All participants’ data were  
 958 registered to the fsaverage template.

959 **Voxel Selection.** Voxel selection followed the criteria in (Tuckute et al., 2023). We retained voxels  
 960 within a superior temporal and posterior parietal mask if they met two conditions: (1) significant  
 961 sound vs. silence response ( $p < 0.001$ , uncorrected), and (2) reliable responses to sounds across  
 962 scan sessions, quantified as:

972  
973  
974  
975

$$r = 1 - \frac{\|\mathbf{v}_{12} - \text{proj}_{\mathbf{v}_3} \mathbf{v}_{12}\|_2}{\|\mathbf{v}_{12}\|_2}, \quad \text{with} \quad \text{proj}_{\mathbf{v}_3} \mathbf{v}_{12} = \left( \frac{\mathbf{v}_3 \cdot \mathbf{v}_{12}}{\|\mathbf{v}_3\|_2^2} \right) \mathbf{v}_3$$

976  
977  
978  
979  
980  
981  
982  
983  
984  
985  
986  
987  
988  
989  
990  
991  
992  
993  
994  
995  
996  
997  
998  
999  
1000  
1001  
1002  
1003  
1004  
1005  
1006  
1007  
1008  
1009  
1010  
1011  
1012  
1013  
1014  
1015  
1016  
1017  
1018  
1019  
1020  
1021  
1022  
1023  
1024  
1025

Here,  $\mathbf{v}_{12}$  is the voxel’s response vector (averaged over the first two sessions) to all 165 sounds, and  $\mathbf{v}_3$  is the same voxel’s response from the third session. This measure captures the fraction of variance in  $\mathbf{v}_{12}$  explained by  $\mathbf{v}_3$ . Voxels with  $r \geq 0.3$  were retained. Across participants, this yielded 7,694 voxels (mean per participant: 961.75; range: 637–1,221).

## C.2 B2021

The B2021 fMRI dataset used in this study was originally collected and analyzed by (Boebinger et al., 2021) and reanalyzed in (Tuckute et al., 2023). We summarize the methodological details below.

**Participants and Experimental Design.** Twenty right-handed participants (14 female; mean age: 25 years, range: 18–34) each completed three fMRI sessions (~2 hours per session). Half of the participants ( $n = 10$ ) were highly trained musicians, with an average of 16.3 years (SD = 2.5) of formal training that began before age 7 and continued through the time of scanning. The other half ( $n = 10$ ) were non-musicians with fewer than 2 years of musical training, none of which occurred before age 7 or within 5 years of scanning. All participants provided informed consent, and the study was approved by the MIT Committee on the Use of Humans as Experimental Subjects (protocol number 2105000382).

**Stimuli.** The stimulus set consisted of 192 natural sounds, including 165 from (Norman-Haignere et al., 2015) and 27 additional music and drumming clips representing diverse musical cultures. To ensure comparability with NH2015, all analyses in this study were restricted to the shared subset of 165 sounds.

**fMRI Procedure.** The scanning procedure closely followed that of (Norman-Haignere et al., 2015), with some modifications. Each stimulus block consisted of three repetitions of a 2-second sound, lasting 10.2 seconds total (TR = 3.4 s, 3 repetitions). Each participant completed 48 runs across the 3 sessions (16 runs per session), with each run containing 24 stimulus blocks and 5 randomly interleaved silent blocks. This design enabled each sound block to be repeated 6 times across the experiment. Participants performed an intensity discrimination task, pressing a button upon detecting the quietest of the three repetitions in a block (12 dB lower).

**Data Acquisition.** MRI data were collected using a 3T Siemens Prisma scanner with a 32-channel head coil at the Athinoula A. Martinos Imaging Center at MIT. Functional volumes (48 slices per volume) covered the superior temporal and parietal lobes, matching the anatomical mask used in (Norman-Haignere et al., 2015). Imaging parameters were: TR = 3.4 s (TA = 1 s), TE = 33 ms, flip angle = 90°, in-plane resolution = 2.1 mm, slice thickness = 3 mm (10% gap), and voxel size = 2.1 × 2.1 × 3.3 mm. A multiband SMS factor of 4 was used to accelerate acquisition. Structural T1 images (1 mm isotropic) were also collected.

**Preprocessing.** Preprocessing matched the pipeline used in (Norman-Haignere et al., 2015), but with a general linear model used to estimate voxel responses due to the shorter stimulus blocks and increased overlap in BOLD responses. For each stimulus block, beta weights were computed using a boxcar function convolved with a canonical hemodynamic response function, along with 6 motion regressors and a linear trend term. Resulting beta weights were downsampled to a 2-mm isotropic grid on the FreeSurfer cortical surface. Each participant’s cortical surface was registered to the fsaverage template.

**Voxel Selection.** Voxels were selected using the same reliability-based procedure described in (Tuckute et al., 2023). Reliability was computed from vectors of beta weights for the 165 shared stimuli, estimated separately from two halves of the data ( $v_1$  = runs 1–24,  $v_2$  = runs 25–48):

1026

$$1027 \quad r = 1 - \frac{\|\mathbf{v}_{12} - \text{proj}_{\mathbf{v}_3} \mathbf{v}_{12}\|_2^2}{\|\mathbf{v}_{12}\|_2^2}, \quad \text{where} \quad \text{proj}_{\mathbf{v}_3} \mathbf{v}_{12} = \left( \frac{\mathbf{v}_3 \cdot \mathbf{v}_{12}}{\|\mathbf{v}_3\|_2^2} \right) \mathbf{v}_3$$

1028

1029 Voxels with  $r \geq 0.3$  and significant sound-evoked responses ( $p < 0.001$ , uncorrected) were retained.  
 1030 This procedure yielded a total of 26,792 reliable voxels across 20 participants (mean: 1,340 per  
 1031 participant; range: 1,020–1,828).

1032

1033

### 1034 C.3 VOXELWISE RESPONSE MODELING

1035

1036 This procedure was repeated 10 times (once per train-test split), and the median corrected vari-  
 1037 ance explained was reported for each voxel-layer pair. We evaluated all layers from each candidate  
 1038 model on both datasets, yielding voxelwise explained variance values for 7,694 voxels (NH2015)  
 1039 and 26,792 voxels (B2021).

1040

1041

**1042 Regularized linear regression and cross-validation.** To model the relationship between model  
 1043 unit activations and measured brain responses, we used voxelwise linear encoding models. For  
 1044 each voxel, we predicted its time-averaged response to natural sounds as a linear combination of  
 1045 time-averaged activations from a specific model layer. We randomly split the 165 sounds into 10  
 1046 unique train-test partitions of 83 training and 82 test sounds. For each split, we fit a regularized  
 1047 linear regression (ridge regression) model using the 83 training sounds and evaluated prediction  
 1048 performance on the held-out 82 sounds.

1049

1050

1051

1052

1053

1054

1055

1056

1057

1058

1059

1060

1061

1062

1063

1064

1065

1066

1067

1068

1069

1070

1071

1072

1073

1074

1075

1076

1077

1078

1079

**1043 Regularized linear regression and cross-validation.** To model the relationship between model  
 1044 unit activations and measured brain responses, we used voxelwise linear encoding models. For  
 1045 each voxel, we predicted its time-averaged response to natural sounds as a linear combination of  
 1046 time-averaged activations from a specific model layer. We randomly split the 165 sounds into 10  
 1047 unique train-test partitions of 83 training and 82 test sounds. For each split, we fit a regularized  
 1048 linear regression (ridge regression) model using the 83 training sounds and evaluated prediction  
 1049 performance on the held-out 82 sounds.

**1050 Regression formulation.** Let  $\mathbf{y} \in \mathbb{R}^n$  be the voxel’s mean response to  $n = 83$  sounds, and let  
 1051  $\mathbf{X} \in \mathbb{R}^{n \times d}$  be the matrix of  $d$  regressors (i.e., time-averaged activations from a model layer). The  
 1052 ridge solution is:

$$1053 \quad \mathbf{w} = (\mathbf{X}^\top \mathbf{X} + n\lambda \mathbf{I})^{-1} \mathbf{X}^\top \mathbf{y}$$

1055 where  $\lambda$  is the regularization parameter and  $\mathbf{w}$  is the vector of regression weights. Both  $\mathbf{y}$  and  
 1056 the columns of  $\mathbf{X}$  were demeaned (but not normalized) prior to regression. This allowed units with  
 1057 greater magnitude variance to contribute more to the prediction under a non-isotropic Gaussian prior.  
 1058 To avoid data leakage, all transformations were learned on the training set and applied to the test set.

1059 We used leave-one-out cross-validation within the 83 training sounds to select  $\lambda$ . For each of 100  
 1060 logarithmically spaced values (from  $10^{-50}$  to  $10^{49}$ ), we computed the mean squared error of the  
 1061 predicted response for each left-out training sound. The  $\lambda$  minimizing this error was used to retrain  
 1062 the model on all 83 training sounds. The final model was then used to predict responses to the  
 1063 82 held-out test sounds, and performance was quantified using the Pearson correlation between  
 1064 predicted and actual voxel responses. Negative correlations or correlations with zero variance were  
 1065 set to zero.

1066 **1067 Correcting for reliability of predicted voxel responses.** Because both training and test responses  
 1068 are affected by measurement noise, we corrected for the reliability of both the predicted and mea-  
 1069 sured voxel responses. This correction was essential to fairly compare model performance across  
 1070 voxels and model layers. We defined the corrected variance explained using the attenuation-  
 1071 corrected squared correlation:

$$1072 \quad r_{\mathbf{v}, \hat{\mathbf{v}}}^2 = \frac{r(\mathbf{v}_{123}, \hat{\mathbf{v}}_{123})^2}{r'_v r'_{\hat{v}}}$$

1073 where  $\mathbf{v}_{123}$  is the voxel response to the 82 test sounds,  $\hat{\mathbf{v}}_{123}$  is the predicted response, and  $r'_v, r'_{\hat{v}}$  are  
 1074 the reliabilities of the measured and predicted responses, respectively. Reliability was estimated via  
 1075 median Spearman–Brown corrected correlations across scan pairs. For stability, we excluded voxels  
 1076 for which  $r'_v$  or  $r'_{\hat{v}}$  was less than  $k = 0.182$  and  $k = 0.183$ , respectively (corresponding to  $p < 0.05$   
 1077 thresholds for 83- and 82-dimensional Gaussian variables).

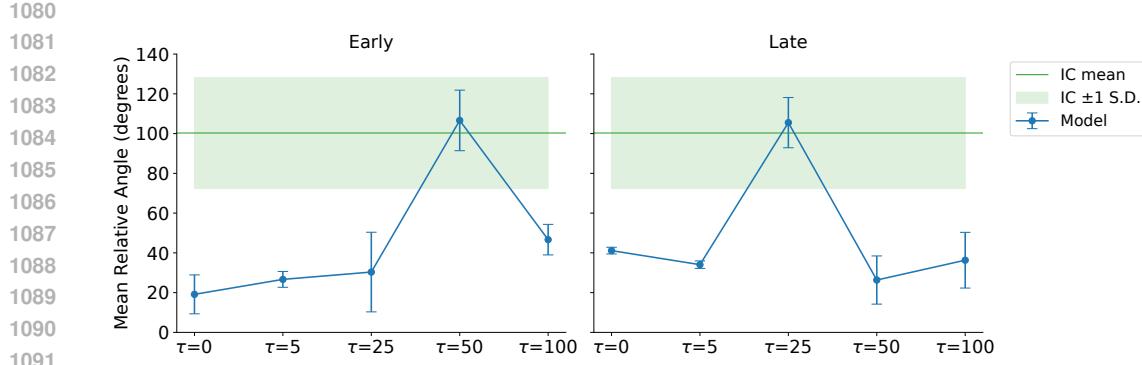


Figure 6: A stronger topographic constraint yields more perpendicular gradients for tonotopy and modulation frequency until  $\tau = 50, 25$  for early and late layers respectively.

#### D ANALYSING PERPENDICULARITY OF GRADIENTS FOR TONOTOPY VERSUS MODULATION RATE

It is known from Baumann et al. (2011) and Baumann et al. (2015) that the gradient of modulation rate and tonotopy run perpendicularly to each other in the auditory cortex. To check for this property in our topographic audio models, we adopted the method specified in the supplementary material of Baumann et al. (2011) which involves performing a planar regression on each 2D preference map, extracting the direction of the steepest gradient from the fitted plane, and computing the relative angle between the tonotopic and AM-rate gradients. For both early and late layers, we observe that a stronger topographic constraint yields more perpendicular gradients – and hence a better match with the actual data from the Inferior Colliculus (IC) (marked in green as IC mean and IC std in Figure 6). We also observe that after a certain threshold, the angles between the gradients start decreasing again.

**LLM usage in work.** LLMs were used for editing grammar, spelling, and suggesting revisions for clarity in the writing.