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# Research Paper A parcellation-based model of the auditory network

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#### ABSTRACT

*Introduction:* The auditory network plays an important role in interaction with the environment. Multiple cortical areas, such as the inferior frontal gyrus, superior temporal gyrus and adjacent insula have been implicated in this processing. However, understanding of this network's connectivity has been devoid of tractography specificity.

*Methods:* Using attention task-based functional magnetic resonance imaging (MRI) studies, an activation likelihood estimation (ALE) of the auditory network was generated. Regions of interest corresponding to the cortical parcellation scheme previously published under the Human Connectome Project were corregistered onto the ALE in the Montreal Neurological Institute coordinate space, and visually assessed for inclusion in the network. Diffusion spectrum MRI-based fiber tractography was performed to determine the structural connections between cortical parcellations comprising the network.

*Results:* Fifteen cortical regions were found to be part of the auditory network: areas 44 and 8C, auditory area 1, 4, and 5, frontal operculum area 4, the lateral belt, medial belt and parabelt, parietal area F centromedian, perisylvian language area, retroinsular cortex, supplementary and cingulate eye field and the temporoparietal junction area 1. These regions showed consistent interconnections between adjacent parcellations. The frontal aslant tract was found to connect areas within the frontal lobe, while the arcuate fasciculus was found to connect the frontal and temporal lobe, and subcortical U-fibers were found to connect parcellations within the temporal area. Further studies may refine this model with the ultimate goal of clinical application.

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#### 1. Introduction

With advances in neuroimaging techniques, clinicians and scientists have discovered that the cerebrum is composed of complex neural networks (Beckmann et al., 2005; De Luca et al., 2006; Thirion et al., 2006). It is thought that the auditory net-

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work is contained within sections of the lateral superior temporal gyrus, planum polare, planum temporale, Heschl's gyri, and the posterior insula (Beckmann et al., 2005; Nourski et al., 2014; Guéguin et al., 2007). These association areas play roles in the convergence and integration of other sensory modalities (Nourski and Howard, 2015). Furthermore, the auditory network allows interaction with the environment which ranges from processing auditory information to other sensory and cognitive tasks, including tonal (Zatorre and Gandour, 2008), pitch (Cha et al., 2016), speech (Giraud et al., 2007), and language processing (Morillon et al., 2010). These areas of the cerebral cortex appear to activate bilaterally, but the network seems to be left-hemisphere dominant (Shaw et al., 2013). Therefore, the auditory network appears to be more complex than originally thought, extending beyond its simple "home" within the Sylvian fissure. While neurosurgeons can preserve the primary cortical functions by sparing the primary visual



Abbreviations: A1, primary auditory cortex; AF, arcuate fasciculus; ALE, activation likelihood estimation; DSI, fiffusion spectrum magnetic resonance imaging; FAT, frontal aslant tract; fMRI, functional magnetic resonance imaging; FOP4, frontal opercular area 4; HCP, Human Connectome Project; LBelt, lateral belt; MBelt, medial belt; MNI, Montreal Neurological Institute; PBelt, parabelt; PFcm, parietal F, region cm; PSL, perisylvian language area; RI, retroinsular cortex; ROIs, region of interests; SCEF, supplementary and cingulate eye field; STSdp, superior temporal sulcus dorsal posterior; TPOJ1, temporal-parietal-occipital junction 1.

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and motor cortex during brain surgery, preservation of a higher cognitive network has proven to be challenging (Burks et al., 2017). Therefore, it is likely that advances in brain tumor surgery can be made by improving the understanding of network connectivity.

Despite the extensive research devoted to the auditory network, most anatomical and functional studies have focused on animal or post-mortem models due to difficulty in obtaining in vivo results in humans (Hackett, 2015). Furthermore, studies have shown interhemispheric and interindividual variabilities in the transverse gyrus among postmortem brain specimens (Rademacher et al., 1993; Rademacher et al., 2001) and MRI (Penhune et al., 1996; Leonard et al., 1998). In addition, the extent of the cytoarchitectonic features along Heschl's gyrus are subject to interhemispheric and interindividual variations (Morosan et al., 2001). This has led to existing models of the auditory network lacking reproducible anatomical nomenclature which could have been used to compare results between studies and allow practical transference of the findings into the field of medicine. (Nourski et al., 2014; Oishi et al., 2011; Dick et al., 2019). However, as the field of neuroscience has moved towards a more comprehensive understanding of brain connectomics and functional neuroimaging, it has become possible to describe more accurate structural and functional models of key cortical networks.

In this study, we constructed a model of the auditory network based on the cortical parcellation scheme published by the Human Connectome Project (HCP). Using relevant task-based functional magnetic resonance imaging (fMRI) studies and BrainMap (http://www.brainmap.org/), a collection of open-access software programs used to generate activation likelihood estimations (ALE) from fMRI data, we identified the primary cortical areas involved in the auditory network. After identifying these regions of interest, we performed Diffusion spectrum MRI-based (DSI) fiber tractography to determine the structural connections between parcellations of the network. Our goal is to provide a more detailed model of structural connectivity of the auditory network for use in future studies.

# 2. Methods

#### 2.1. Literature search

We searched BrainMap Sleuth 2.4 (Research Imaging Institute of Texas Health Science Center San Antonio) on July 24, 2017, for all relevant task-based fMRI studies related to audition in healthy individuals. We also queried PubMed on July 12, 2017, for the fMRI studies relevant to the network. The following search algorithm was used: "Audition OR Activations Only OR Normal AND fMRI." The search returned 101 papers which were reviewed for inclusion in this study based on the following inclusion criteria: (1) peer-reviewed publication, (2) task-based fMRI study related to the auditory network and audition, (3) based on wholebrain, voxel-wise imaging, (4) including standardized coordinatebased results in the Talairach or Montreal Neuroimaging Institute (MNI) coordinate space, and (5) including at least one healthy human control cohort. Only coordinates from healthy subjects were utilized in our analysis. Region of interest studies, meta-analyses, resting-state studies, and studies examining interactions between two or more networks were excluded. Overall, 73 papers met criteria for inclusion in this study (Fiez et al., 1995; Grahn and Rowe, 2009; Grahn and McAuley, 2009; Grahn and Brett, 2007; Kiehl and Liddle, 2001; Chouinard and Paus, 2006; Mazard et al., 2002; Nunn et al., 2002; Sevostianov et al., 2002; Stevens et al., 2000; Toyomura et al., 2007; Finger et al., 2006; Hart et al., 2004; Mitchell et al., 2003; Calhoun et al., 2006; Friederici et al., 2010; Griffiths et al., 1998; Griffiths et al., 2000; Wildgruber et al., 2002; Chang et al., 2009; Meyer et al., 2005; Seifritz et al., 2003; Wheeler et al., 2000; Dick et al., 2007; Luc et al., 2008; Galati et al., 2008; Horovitz et al., 2002; Jobard et al., 2007; Jager et al., 2006; Ackermann et al., 2001; Gervais et al., 2004; Lockwood et al., 1999; Hesling et al., 2010; Abutalebi et al., 2007; Brammer et al., 1997; Gandour et al., 2002; Langheim et al., 2002; Peters et al., 2007; Szameitat et al., 2002; Sharp et al., 2010; Christoffels et al., 2007; Mathiak et al., 2004; Specht and Reul, 2003; Specht et al., 2005; Isenberg et al., 2012; Jäncke et al., 1998; Thivard et al., 2000; Bangert et al., 2006; Rao et al., 1997; Suzuki et al., 2002; Wong et al., 2008; Wilson et al., 2004; Belin et al., 2000; Celsis et al., 1999; Leff et al., 2008; van Dijk and Backes, 2003; Buchsbaum et al., 2005; Binder et al., 1996; Binder et al., 2000; Jardri et al., 2007; Postle and Hamidi, 2007; Brown et al., 2004; Bense et al., 2001; Lattner et al., 2005; Baumgartner et al., 2006; Husain et al., 2006a, 2006b; Rinne et al., 2005; Fu et al., 2006; Saito et al., 2006; Bilecen et al., 2002; Tourville et al., 2008; Rao et al., 2001; Rademacher et al., 2001; Penhune et al., 1996; Leonard et al., 1998; Morosan et al., 2001; Oishi et al., 2011; Dick et al., 2019; Fiez et al., 1995; Grahn and Rowe, 2009; Grahn and McAuley, 2009; Grahn and Brett, 2007; Kiehl and Liddle, 2001; Chouinard and Paus, 2006; Mazard et al., 2002; Nunn et al., 2002; Sevostianov et al., 2002; Stevens et al., 2000; Toyomura et al., 2007; Finger et al., 2006; Hart et al., 2004; Mitchell et al., 2003; Calhoun et al., 2006; Friederici et al., 2010; Griffiths et al., 1998; Griffiths et al., 2000; Wildgruber et al., 2002; Chang et al., 2009; Meyer et al., 2005; Seifritz et al., 2003; Wheeler et al., 2000; Dick et al., 2007; Luc et al., 2008; Galati et al., 2008; Horovitz et al., 2002; Jobard et al., 2007; Jager et al., 2006; Ackermann et al., 2001; Gervais et al., 2004; Lockwood et al., 1999; Hesling et al., 2010; Abutalebi et al., 2007; Brammer et al., 1997; Gandour et al., 2002; Langheim et al., 2002; Peters et al., 2007; Szameitat et al., 2002; Sharp et al., 2010; Christoffels et al., 2007; Mathiak et al., 2004; Specht and Reul, 2003; Specht et al., 2005; Isenberg et al., 2012; Jäncke et al., 1998; Thivard et al., 2000; Bangert et al., 2006; Rao et al., 1997; Suzuki et al., 2002; Wong et al., 2008; Wilson et al., 2004; Belin et al., 2000; Celsis et al., 1999; Leff et al., 2008; van Dijk and Backes, 2003; Buchsbaum et al., 2005; Binder et al., 1996; Binder et al., 2000; Jardri et al., 2007; Postle and Hamidi, 2007; Brown et al., 2004; Bense et al., 2001; Lattner et al., 2005; Baumgartner et al., 2006; Husain et al., 2006a, 2006b).

# 2.2. Creation of 3D regions of interest

Diffusion-weighted MRI data were obtained from the publicly available HCP (Glasser et al., 2013; Glasser et al., 2016). Their images were acquired using a 3T Siemens, wherein one 3D T1w MPRAGE image and one 3D T2w SPACE image was acquired at 0.7mm isotropic resolution. Whole-brain resting-state fMRI data and field maps were also acquired. The field maps were used to enable accurate cross-modal registrations of the T2w and fMRI images to the T1w image for each subject. Additionally, a spin echo phase was used to reverse images acquired during the fMRI session to compute a more accurate fMRI bias field correction and to segment regions of gradient-echo signal loss.

In the original HCP study, diffusion-weighted MRI data were studied in CIFTI file format. CIFTI files involve a surface-based coordinate system, termed greyordinates, which localizes regions of interest (ROIs) on inflated brains (Van Essen and Glasser, 2016). This is in contrast to traditional file formats, such as NIFTI, which denote regions based on volumetric dimensions (Larobina and Murino, 2014). As a result, it was difficult to perform deterministic fiber tractography using ROIs in CIFTI file format. To convert the parcellation file to volumetric coordinates, the relevant greyordinate parcellation fields were standardized to the three-dimensional volumetric working spaces of DSI Studio (Carnegie Mellon, http:

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//dsi-studio.labsolver.org) using structural imaging data available through the HCP. This operation was formed using the Connectome Workbench command-line interface (Van Essen laboratory, Washington University 2016). A single, volumetric ROI was generated for the parcellations identified in the original HCP study (Glasser et al., 2016).

# 2.3. Activation likelihood estimation generation and identification of relevant cortical regions

We used BrainMap Ginger ALE 2.3.6 to extract the relevant fMRI data from our literature search to create an activation likelihood estimation (ALE) of the auditory network (Husain et al., 2006b; Rinne et al., 2005; Fu et al., 2006). All Talairach coordinates identified during the literature review were converted to the MNI coordinate space using SPM Conversion in GingerALE. We subsequently performed a single study analysis using cluster-level interference in the MNI coordinate space (cluster level of 0.05, threshold permutations of 1,000, uncorrected p-value of 0.001). The ALE coordinate data were displayed on an MNI-normalized template brain using the Multi-image Analysis GUI (Mango) 4.0.1 (ric.uthscsa.edu/mango). The pre-constructed ROIs of the parcellations were then overlaid on the ALE and compared visually for inclusion in the network.

# 2.4. Network tractography

Working from the hypothesis that functionally connected regions of a network are likely structurally connected, we proceeded to determine the backbone of the network using deterministic tractography. All fiber tractography was done in DSI Studio (http://dsi-studio.labsolver.org) using publicly available brain imaging from the Human Connectome Project (http://humanconnectome.org, release Q3). Tractography was performed individually with 25 healthy, unrelated subjects (Subjects IDs: MGH\_1001, MGH\_1002, MGH\_1003, MGH\_1004, MGH\_1005, MGH\_1006, MGH\_1007, MGH\_1008, MGH\_1009, MGH\_1010, MGH\_1011, MGH\_1012, MGH\_1013, MGH\_1014, MGH\_1015, MGH\_1016, MGH\_1017, MGH\_1018, MGH\_1019, MGH\_1020, MGH\_1021, MGH\_1022, MGH\_1023, MGH\_1024, MGH\_1025). A multi-shell diffusion scheme was used, with b-values of 990, 1,985, and 1,980 s/mm<sup>2</sup>. Each b-value was sampled in 90 directions. The in-plane resolution was 1.25 mm. The diffusion data were reconstructed using generalized q-sampling imaging with a diffusion sampling length ratio of 1.25 (Saito et al., 2006).

All brains were registered to the Montreal Neurological Institute (MNI) coordinate space, with imaging warped to fit a standardized brain model comparison between subjects (Evans et al., 1992). Tractography was performed in DSI Studio (Carnegie Mellon, http://dsi-studio.labsolver.org) using a region of interest approach to initiate fiber tracking from a user-defined seed region (Martino et al., 2013). A two-ROI approach was used to isolate tracts (Kraft et al., 2011)

Voxels within each ROI were automatically traced with a maximum angular threshold of 45°. When a voxel was approached with no tract direction or a direction greater than 45°, the tract was halted. Tracts with length longer than 800 mm were discarded. In some instances, exclusion ROIs were placed to exclude spurious tracts that were not involved in the white matter pathway of interest.

#### 2.5. Measuring connection strength

To quantify the strength of the connections identified within the auditory network across all subjects, the tracking parameters used within DSI Studio were modified such that the program



**Fig. 1.** Activation likelihood estimation (ALE) of 73 task-based fMRI experiments related to auditory processing. The three-dimensional ALE data (in red) are displayed in Mango on a brain normalised to the MNI coordinate space. (a) ALE data highlighting the unilateral left-sided inferior frontal gyrus and bilateral temporal lobes and adjacent insula. (b) ALE data highlighting the left inferior frontal lobe and temporal gyrus and adjacent insula. (c) ALE data highlighting the inferior frontal gyrus. (d) ALE data highlighting the area of middle frontal gyrus.

would count the total number of tracts between any two ROIs based on a random seed count of 2.5 million. Working sequentially through ROI pairs in the network, the number of tracts between regions was recorded for each of the 25 subjects after fiber tractography was terminated under these new conditions. The strengths of the connections within the auditory network were calculated by averaging the number of tracts between each ROI pair of the network across all subjects.

#### 3. Results

#### 3.1. ALE regions and corresponding parcellations

Fig. 1 demonstrates the ALE of the 73 auditory-related, taskbased fMRI experiments included in our meta-analysis. Highlighted areas include the frontal and temporal lobes, specifically the inferior frontal gyrus, medial frontal gyrus, superior temporal gyrus, adjacent insula, and posterior temporal lobe. Fifteen regions of interest were found to overlap the fMRI data, including A1, A4, A5, LBelt, PBelt, RI, PFcm, PSL, STSdp, TPOJ1, 44, FOP4, 8C, and SCEF. Comparison overlays between these cortical regions and the ALE are shown in Fig. 2.

# 3.2. Structural connectivity of the auditory network

Deterministic tractography was utilized to determine the basic structural connectivity of the auditory network. These results are shown in Fig. 3. Individual connections within this network are presented in the supplemental Table 1 which tabulates the strengths of individual connection.

The cortical areas comprising the auditory network can be classified based on the area of the brain to which they localize: superior temporal gyrus and adjacent insula (A1, A4, A5, LBelt, MBelt, PBelt, RI), posterior temporal lobe (PFcm, PSL, STSdp, TPOJ1), medial frontal gyrus (8C and SCEF), and inferior frontal gyrus (44 and FOP4).

The frontal aslant tract (FAT), as shown in purple (Fig. 3), connects the inferior frontal gyrus, the superior frontal gyrus, and the



**Fig. 2.** Comparison overlays between cortical parcellations (shown in blue) and the activation likelihood estimation (shown in red) from Figure 1 in the left cerebral hemisphere. Regions were visually assessed for inclusion in the network if they overlapped with the activation likelihood estimation data. Cortical parcellation assessed for inclusion in our model of the auditory network included area A1, A4, A5, LBelt, MBelt, PBelt, and RI of the superior temporal gyrus and adjacent insula; PFcm, PSL, STSdp, and TPOJ1 of the posterior temporal lobe; regions 44 and FOP4 of the inferior frontal gyrus; and regions 8C and SCEF of the middle frontal gyrus. Labels indicate the region of interest shown in each panel.

middle frontal gyrus of the auditory network. Connections between the inferior frontal gyrus (44 and FOP4) and medial frontal areas (8C and SCEF) were observed. These fibers originate from the inferior frontal gyrus and course inferiorly to the white matter. They run superiorly and posteriorly to the middle frontal area, where 8C and SCEF are located.

Subcortical U-fibers, as shown in pink (Fig. 3), connect the superior temporal gyrus and the posterior temporal lobe within the auditory network. The connections between the superior temporal areas (A1, A4, A5, LBelt, MBelt, PBelt, RI) and posterior temporal areas (PFcm, PSL, STSdp, TPOJ1) were identified. These fibers orig-

inate from the superior temporal gyrus and adjacent insula. They course inferiorly into the deep white matter of Heschl's gyrus and curve posteriorly and superiorly into the posterior temporal area, where PFcm, PSL, STSdp, and TPOJI are located.

The arcuate fasciculus (AF), as shown in green (Fig. 3), connects frontal areas and temporal areas in the auditory network. In general, connections of the AF within the auditory network can be divided into four subtypes: inferior frontal gyrus to superior temporal gyrus, inferior frontal gyrus to the posterior temporal lobe, medial frontal gyrus to superior temporal gyrus, and medial frontal gyrus to the posterior temporal lobe. Connections between medial



**Fig. 3.** Tractography model of the auditory network as shown on T1 -weighted magnetic resonance image in the left cerebral hemisphere. FIRST ROW: sagittal sections from most medial to most lateral demonstrating the extent of the arcuate fasciculus which projects between the frontal and temporal regions of the auditory network. SECOND ROW: coronal sections from most anterior to posterior highlighting the projections between inferior to middle frontal gyrus via frontal aslant tract within the auditory network. THIRD ROW: coronal sections from most anterior to posterior highlighting the subcortical U-fibres within the temporal region of the auditory network. FOURTH ROW: axial sections from most superior to inferior highlighting the arcuate fasciculus and frontal aslant tract within the auditory network.



Anterior

Posterior

Fig. 4. Simplified schematic of the white matter connections identified between individual parcellations of the auditory network during fiber tracking analysis. Connections are labels with their average strength measured across all 25 subjects used in this analysis.

frontal gyrus (8C and SCEF) and posterior temporal areas (PFcm, PSL, STSdp, TPOJ1) were also identified. These fibers course inferiorly into the deep white matter of the medial frontal gyrus before curving 90 degrees to continue in the anterior-posterior direction. The fibers pass deep into the sensorimotor cortex before curving laterally to terminate in the temporal cortex corresponding to areas PFcm, PSL, STSdp, and TPOJ1. Connections between inferior frontal (44 and FOP4) and posterior temporal areas (PFcm, PSL, STSdp, TPOJ1) were also noted. In addition, connections between superior temporal gyrus (A1, A4, A5, LBelt, MBelt, PBelt, RI) to medial frontal areas (8C and SCEF) were identified. Connections between superior temporal gyrus (A1, A4, A5, LBelt, MBelt, PBelt, RI) and inferior frontal gyrus (44 and FOP4) were observed. The connections of the auditory network are summarized in Fig. 4. Lines in this schematic represent individual connections of the auditory network, which are labelled with their average strength as measured across all 25 subjects included in this analysis.

# 4. Discussion

The auditory network has long been described in terms of core, belt, and parabelt regions (Kaas and Hackett, 2000; Hackett et al., 1998). The core of the auditory network has been localized to the posteromedial two-thirds of Heschl's Gyrus (Nourski et al., 2014; Guéguin et al., 2007). The belt and parabelt regions, associated with parcellations MBelt, LBelt, and PBelt, have not been as well characterized. These regions are largely based on non-human primate studies rather than true human anatomy (Hackett, 2015).

In this study, we utilized meta-analytic software and deterministic tractography to construct a model of structural connectivity of the auditory network based on the cortical parcellation scheme published previously under the Human Connectome Project (Glasser et al., 2016). We used a meta-analytic approach to try to minimize between-study differences to develop a consensus data with as much statistical power as the literature allows. Additionally, linking these data points to a standard coordinate scheme, such as the HCP atlas, facilitates comparison between studies. Further, by linking functional data to anatomically precise areas, the findings can be directly clinically applicable. We believe that a better understanding of the cortical areas and tracts involved in the auditory network can improve neurosurgeons' ability to preserve this network's function in surgery. The anatomic constituents of this network are discussed below.

# 4.1. The anatomic model

## 4.1.1. Superior temporal gyrus and adjacent insula

The superior temporal gyrus and adjacent insula have been shown to be a component of auditory processing, with underlying language functions, including reception, perception, inner speech, and auditory imagery (Gernsbacher and Kaschak, 2003; Shergill et al., 2000; Liégeois-Chauvel et al., 2004). We found that regions A1, A4, A5, MBelt, PBelt, LBelt, and RI overlap with the auditory network in the area of the superior temporal gyrus and adjacent insula. Our ALE also shows bilateral activation of the superior temporal gyrus, which is consistent with other studies (Dick et al., 2007; Abutalebi et al., 2007; Bilecen et al., 2002).

A1 is known as the primary auditory cortex and is located on the superior temporal gyrus of the temporal lobe (Baker et al., 2018a). A1 is crucial for the initial processing of auditory stimuli, and is involved in the detection and extraction of basic acoustic signal features, such as frequency, lateralization, onset time, synchronicity, modulation coherence, loudness, and harmonicism (Wong et al., 2008; Langers et al., 2007). Areas A4 and A5 are newly described parcellations from the auditory association cortex, and unlike A1, they involve more in various associating functions rather than pure auditory functions (Glasser et al., 2016). A4 is on the superior surface of the posterior half of the superior temporal gyrus and may correspond to previously described cytoarchitectonic area Te3 (Baker et al., 2018a; Morosan et al., 2005). There is evidence that this region of the brain processes perceptual and conceptual acoustic sound. It has the auditory function of encoding sentences and decoding melodies (Albouy et al., 2020). Furthermore, A4 is regarded as the "grammatical" area, as it stores learned sentence structures (Knoblauch et al., 2004). A5 is a thin anterior-posterior running strip on the superior lateral surface of the posterior portion of the superior temporal gyrus (Baker et al., 2018a). This region of the brain processes perceptual and conceptual acoustic information (Trumpp et al., 2013).

The medial belt (MBelt), lateral belt (LBelt) and parabelt (PBelt) are newly described brain parcellations from the auditory cortex (Glasser et al., 2016). These three complexes were surrounding the auditory core, with the MBelt and LBelt being heavily myelinated (Glasser et al., 2016). These HCP defined parcellations are similar, but not identical to parcellations that have been previously identified in this area (Moerel et al., 2014). Additionally, the HCP identified PBelt as a lateral parabelt complex and area 52 medial to the MBelt, wherein previous literature has suggested area 52 corresponds to the MBelt (Moerel et al., 2014). The arrangement of these areas is similar to that of Von Economo and Koskinas, with their TB corresponding to the MBelt and LBelt and their TA1 corresponding to the HCP's PBelt (Triarhou, 2007a, 2007b).

The MBelt runs on the medial surface of Heschl's gyrus. Little information has been gathered on the medial belt (Baker et al., 2018a, 2018b), however it is known that its neurons respond to complex sounds (Recanzone et al., 2000; Rauschecker et al., 1995; Schroeder et al., 2001). MBelt has the function of auditory spatial reception, through the integration of multi-sensations, including somatosensory, visual and auditory stimulations (Schroeder et al., 2001; Groh et al., 2001). The LBelt is located on the lateral surface of Heschl's gyrus (Baker et al., 2018a). Compared to the medial belt, the lateral belt is more well studied because of its greater accessibility to neurophysiological recording (Rauschecker et al., 1995). In contrast to A1, LBelt instead responds to pure tone acoustic stimuli and is suggested to integrate auditory information, given that it is more responsive to noise with a range of frequencies greater than just pure tones (Rauschecker et al., 1997). Lesion studies also prove that the lateral belt has the function of spatial cognition (Romanski et al., 1999a, 1999b). The PBelt is located in the superior surface of the inferior portion of the supramarginal gyrus, which is a small region between the lateral edge of Heschl's gyrus and the opercular cleft of the inferior supramarginal gyrus (Baker et al., 2018a). The exact function of the parabelt, a newly characterized parcellation, is understudied. The parabelt region is located at the plenum temporale and contributes to its auditory processing after perceiving complex sounds, including speech, acoustic patterns, as well as environmental and music sounds (Griffiths and Warren, 2002). The retroinsular cortex (RI) is located anterior superior to the long gyrus of the insula. It is located at the deep termination of Heschl's gyrus at its superomedial termination (Baker et al., 2018a). It has the function of receiving corticocortical afferents regarding somatosensory inputs while serving auditory responses (Chudler et al., 1989; Fu et al., 2003).

Given the role of the superior temporal gyrus and adjacent insula in auditory functioning, it is unsurprising that the parcellations within these areas of the cortex form part of the auditory network. Furthermore, structural and functional connections between parcellations within the superior temporal gyrus suggest the presence of multisensory responses in the auditory areas, which is consistent with other functional studies (Fu et al., 2003; Ghazanfar et al., 2005; Lakatos et al., 2007). Further study is needed to understand the functionalities and relationships between parcellations in auditory networks.

#### 4.1.2. Posterior temporal lobe

The posterior temporal lobe is well-established in the literature as part of the auditory network, and is involved in phonological processing (Shergill et al., 2000; Giraud and Price, 2001; Wise et al., 2001). Cortical areas PFcm, PSL, STSdp, and TPOJ1 overlap with the ALE in the posterior temporal lobe. The ALE constructed for the purposes of this study highlights bilateral activation of the posterior temporal lobe, which has been demonstrated in several other studies (Calhoun et al., 2006; Friederici et al., 2010; Bense et al., 2001).

Parietal F, region cm (PFcm) is located in the superior portion of the supramarginal gyrus. It is primarily located on the opercular cleft of this part of the gyrus (Baker et al., 2018a). Area PFcm is important in processing language with regard to vocabulary, semantics, syllables, tones, and auditory-verbal working memory (Celsis et al., 1999; Howard et al., 1992; Zatorre et al., 1992; Fiez et al., 1996). The perisylvian language area (PSL), a newly described area, is located at the apex of the posterior Sylvian fissure and is in the lower portion of the posterior part of the supramarginal gyru (Baker et al., 2018a). PSL is important for higher cognitive functions such as language perceptual function, information processing, emotion regulation and control of cognitive functions (John et al., 2011; Newhart et al., 2012). Temporal-parietal-occipital junction 1 (TPOI1) is located on the posterior superior temporal sulcus (Baker et al., 2018c). TPOJ1 is a newly described area and its functions are still unclear. However, it is known that the temporalparietal-occipital junction plays a role in high-level neurological functions including generation of language, visuospatial attention, and assimilation of audiovisual information (Vaina, 1994). The superior temporal sulcus dorsal posterior (STSdp) is located on the posterior half of the lateral face of the superior temporal gyrus and the posterior half of the superior bank of the superior temporal sulcus (Baker et al., 2018d). STSdp is a newly described parcellation from the association cortex and fMRI studies show that it is involved in a higher level of activation in various associating functions, rather than pure auditory functions (Glasser et al., 2016). The exact function of STSdp is unknown, however, it is known that the posterior superior temporal sulcus is associated with auditory processing from language inputs and short-term auditory-verbal memory (Fiez et al., 1996; Liebenthal et al., 2010; Binder, 1997).

While area PFcm has been shown to be active during analysis of auditory information and is part of the auditory network in our study, the roles of newly introduced areas including PSL, STSdp, and TPOJ1 in auditory processing are not well characterized. Further functional research is needed to investigate their roles in the auditory network.

#### 4.1.3. Inferior frontal gyrus

The inferior frontal gyrus is well-established in the literature as part of the auditory network (Shergill et al., 2000). Cortical areas 44 and FOP4 overlap with the ALE in the inferior frontal gyrus. The ALE constructed for the purposes of this study demonstrates unilateral left-sided activation of the inferior frontal gyrus, which has been demonstrated in several other studies (Ackermann et al., 2001; Bangert et al., 2006).

Brodmann's area 44 (BA44) is located in the pars opercularis of the inferior frontal lobe (Keller et al., 2009). BA44 is part of Broca's area and primarily implicated in high-level aspects of speech production, as well as potentially involved in imitation, music perception and verbal working memory (Newhart et al., 2012; Bradley et al., 1980; Heiser et al., 2003). FOP4, a newly described area of the brain that was parcellated from the frontal operculum, is located on the inner surface of the pars opercularis of the inferior frontal gyrus (Baker et al., 2018a). It plays key role in the initiation of language and lexical retrieval required for language learning (Li et al., 2017; Steinmetz and Seitz, 1991).

#### 4.1.4. Medial frontal gyrus

Activation of the medial frontal gyrus is associated with auditory functions (Shergill et al., 2000). Cortical areas 8C and SCEF overlap with the ALE in the middle frontal gyrus. The ALE shows that these areas are activated unilaterally in the auditory network, which has been described in several fMRI-related studies (Buchsbaum et al., 2005; Baumgartner et al., 2006).

Area 8C is located at the posterior part of the medial frontal gyrus (Baker et al., 2018b). Area 8C is a newly identified area and its exact function is unclear. However, it is known that Brodmann's area 8 integrates vision with auditory and somatosensory inputs and has a critical role for visuospatial cognition (Reser et al., 2013; Genovesio et al., 2011; Levy and Goldman-Rakic, 1999). It also involves integrating cognitive and limbic information during decision making and error monitoring during attention-demanding task performance (Ray and Zald, 2012; Etkin et al., 2011). The supplementary and cingulate gyrus (SCEF) is located on the posterior medial surface of the superior frontal gyrus (Baker et al., 2018e). It is involved in visual imagery, image generation and working memory (Glasser et al., 2016; Gulyás, 2001; Formisano et al., 2002).

The precise nature of area 8C and SCEF in auditory is not known. However, with the connections between medial frontal gyrus and temporal areas via the arcuate fasciculus, the medial frontal gyrus received comprehensive auditory information from the temporal areas for higher cognitive processing (Saur et al., 2010). Little is known about the auditory dynamics of frontal and temporal areas; further research is needed to understand the interactions between parcellations in the auditory cortex and their roles in cognitive functioning.

#### 4.2. The strength of connections within the auditory network

The average strength of the connections identified between parcellations of the auditory network is reported briefly in Table 1 and in full in Supplementary Table 2. Two different values for strength were computed. The first represents the average strength as measured across 25 subjects used in this analysis; the second represents the average strength when only considering subjects demonstrating connections when performing tractography. Based on these results, it is clear that the structural auditory connectivity varies to some degree between individuals. By presenting both sets of average connectional strengths, we can see how these connections vary in the network.

In this study, we did not set a threshold for the strength for the inclusion criteria for the connections within the network. For example, when evaluating the connection 8C between A4, the average strength across all 25 individuals was measured to be 31 versus 390 in the single subset identified as having this tract. If we had set a threshold of an average strength of 10 or a threshold to the frequency by which we saw the connection, such as in at least 10 subjects, then we would not report their connection in this paper. However, in our view, it is more appropriate to mention that the connection between 8C and A4 is a relatively weak connection that occurs less frequently in the auditory network, as opposed to saying no such connection exists. Despite not setting such a threshold, additional study is required to understand whether the strength and frequency of auditory connections are critical to the functionality of the network.

# 4.3. Limitations

The left auditory cortex is more highly folded and larger than the right (Shaw et al., 2013). In addition, research on unilateral hearing loss indicates greater restructuring of the left auditory cortex in cases of left-sided sensorineural hearing loss compared to

#### Table 1

Structural connectivity strength (number of fibers) between each parcellation within the auditory network for the connections evident in the majority of the tractography population.

Connections	Average Strength of Connection
44 to 8C	571.2
44 to SCEF	232.3
44 to RI	17.1
8C to FOP4	217.2
8C to SCEF	69.4
A1 to A4	319.5
A1 to A5	118.7
A1 to LBelt	729.8
A1 to MBelt	709.2
A1 to PBelt	617
A1 to PFcm	304.3
A1 to PSL	71.9
Al to SISdp	80.6
AT to PL	181.4
	415 1216 /
A4 to I Belt	677 /
A4 to MBelt	568 3
A4 to PBelt	1799.6
A4 to PFcm	389.5
A4 to PSL	451.7
A4 to STSdp	542.9
A4 to TPO[1	441.79
A4 has to RI	456.7
A5 to FOP4	122.4
A5 to LBelt	265.7
A5 to MBelt	486.3
A5 to PBelt	908.9
A5 to PFcm	106.6
A5 to PSL	124.6
A5 to STSdp	1124.8
A5 to IPOJI	463
AD HAS TO KI	65.2
FOP4 to Millert	60.3
FOP4 to PSI	29
FOP4 to SCEF	110
FOP4 to TPOI1	60.3
FOP4 has to RI	45
LBelt to MBelt	329.8
LBelt to PBelt	1339.8
LBelt to PFcm	215.5
LBelt to PSL	109.4
LBelt to STSdp	214.5
LBelt to TPOJ1	194
LBelt has to RI	456.7
WBelt to PECT	טפט 145 ס
MBelt to PSI	145.9
MBelt to STSdp	138.3
MBelt to TPOI1	132.9
MBelt has to RI	325.6
PBelt to PFcm	496.5
PBelt to PSL	259.4
PBelt to STSdp	514.6
PBelt to TPOJ1	345
PBelt has to RI	492.6
PFcm to PSL	853.4
PFcm to STSdp	190
PFcm to TPOJ1	422
PFcm has to RI	785.5
PSL to SISdp	3U3.b
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STSdp to Iroji STSdp has to RI	177 5
TPOI1 has to RI	274 7

healthy controls. No such restructuring was identified in rightsided sensorineural hearing loss (Bilecen et al., 2002). Finally, the auditory hallucinations seen in schizophrenia may relate to either a left-sided temporal lobe abnormality or a potential interhemispheric effect (Eickhoff et al., 2012). Due to the seeming predominance of the left-sided auditory cortex in audition, we focused on building a model of the auditory network solely on the left side. Further research is required to fully describe the connectivity and interrelatedness of the left and right auditory cortices.

Using fMRI data alone also presents another source of potential limitation. Auditory cortices were first investigated using EEG before advancing to positive emission tomography (PET) and eventually fMRI. Since then, the use of fMRI has accelerated due to wide availability, relative safety, and its ability to measure dynamic cerebral activity (Turkeltaub et al., 2012). Studies using fMRI have been shown to be sensitive to variations in loudness and sound intensity (Eickhoff et al., 2009). However, analysis of such data often relies on Talairach or MNI templates, which are based on post-mortem brain studies, or on a small sample size of healthy brain studies. Such issues indicate that the dependence on fMRI may be limited in its scope and alternative methods have been suggested, such as anatomical MRI which has been used in the investigation of primary visual cortices (Yeh et al., 2010). Despite these limitations, our study does provide a preliminary anatomic model on which to base future research.

## 5. Conclusion

We present a preliminary tractographic model of the auditory network. This model comprises parcellation within the frontal and temporal cortex, which are principally linked through the arcuate fasciculus, frontal aslant tract and subcortical U-fibre. Further studies may refine this model with the ultimate goal of clinical application.

#### **Declaration of Competing Interest**

Dr Sughrue is the Chief Medical Officer of Omniscient Neurotechnology, however this does not pose a conflict of interest in this study. The other authors have no conflicts of interest.

#### **CRediT** authorship contribution statement

Joseph J. Kuiper: Investigation, Writing - original draft. Yueh-Hsin Lin: Investigation, Formal analysis. Isabella M. Young: Supervision, Writing - review & editing. Michael Y. Bai: Visualization. Robert G. Briggs: Writing - original draft. Onur Tanglay: Investigation. R. Dineth Fonseka: Conceptualization. Jorge Hormovas: Software. Vukshitha Dhanaraj: Software. Andrew K. Conner: Data curation. Christen M. O'Neal: Resources. Michael E. Sughrue: Conceptualization, Methodology, Supervision.

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# Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.heares.2020.108078.

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