Factors accounting for variation in the degree of contralateral bias in human auditory cortical processing of binaural cues: An fMRI study

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Is auditory space represented primarily in contralateral human auditory cortex?

- Mixed fMRI evidence for (Krumbholz et al. 2005; von Kriegstein et al. 2008) and against (Woldorff et al. 1999; Zimmer et al. 2006) "**contralateral bias**," i.e., enhanced BOLD response in auditory cortex (AC) for sounds carrying contralateral binaural spatial cues: interaural level and time differences ("**ILD**" and "**ITD**").

- Evidence of hemispheric asymmetry in degree of contralateral bias for binaural spatial cues, often interpreted as right hemisphere (RH) specialization for auditory spatial processing (Krumbholz et al. 2005, 2007; Palomaki et al. 2002, 2005; Tiitinen et al. 2006; Johnson & Hautus 2010; Salminen et al. 2010).

Potential reasons for incongruent findings regarding contralateral bias

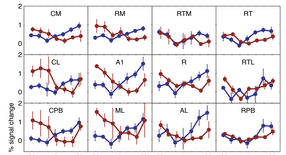
- Varying contralateral bias across binaural spatial cue values (von Kriegstein et al. 2008) and across AC regions; traditional contralaterality indices (CI) often compare response to contra and ipsi sound at limited range of values, averaged across large areas of cortex.

- Influence of stimulus-specific adaptation (Ulanovsky et al. 2003).

- Contralateral bias effect small, difficult to detect (Krumbholz et al. 2005; Werner-Reiss & Groh 2008; Johnson & Hautus 2010).

- Different hemispheric processing relationships/mechanisms for ILD vs ITD (Johnson & Hautus 2010).

ILD tuning curves

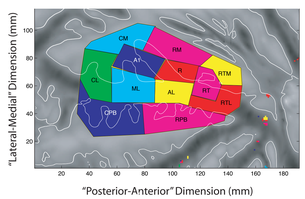


Stecker & McLaughlin 2010

Question: Is contralateral bias reduced for large vs. moderate ILD values?

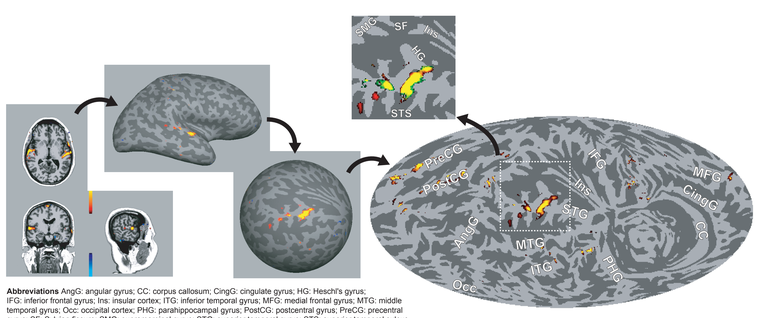
Methods

Subjects	10 (5 female) normal-hearing, right-handed subjects.
Stimuli	1-s narrowband Gabor click trains (4000 Hz carrier frequency, 2-ms interclick interval) varying across ILD (+/-30, 20, 10, 5, 0 dB ILD), or silence (-10 dB). Average binaural level: 80 dB. Presentation rate: 5 trains of 32 clicks/s (5 Hz). Interstimulus interval jittered from 1 - 5-s. Binaural presentation via piezo insert earphones (Sensimetrics) in ear defenders.
Task	Respond to infrequent pitch change (1.2-ms ICI) with right-hand button press.
Design	Event-related design. Continuous carryover paradigm (Aguirre 2007): each stimulus condition presented both preceding and following every other condition. 2 runs of 201 stimulus presentations per subject.
Imaging	BOLD echoplanar imaging (Philips, 3 Tesla). Continuous imaging (TR = 2-s). 42 slices (3 mm), 2.75mm x 2.75mm in-plane resolution.
Analysis	3D functional preprocessing: motion corr., high-pass filtering (100 s) in FSL. Cortical surface extraction (Freesurfer), spherical alignment between subjects. Projection to equal-area map (Mollweide), center on HG x STG, STG on equator. 12 regions of interest (ROI) according to Woods et al. 2010 (primate model). ROI response: mean across all voxels.



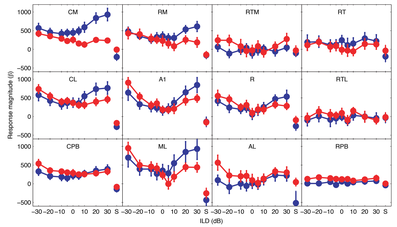
Anatomical ROIs (above) defined on the cortical surface (following Woods et al. 2010) on the basis of comparison to functional fields of macaque AC and relative to (spherically aligned) curvature map in human AC.

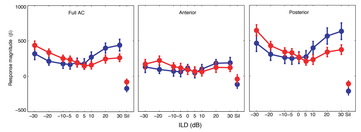
Abbreviations: A1: primary field; AL: anterolateral; CL: caudolateral; CM: caudomedial; CPB: caudal parabelt; ML: mediolateral; R: rostral; RM: rostromedial; RPB: rostral parabelt; RT: rostrotemporal; RTL: rostrotemperolateral; RTM: rostrotemporomedial.



Abbreviations AngG: angular gyrus; CC: corpus callosum; CingG: cingulate gyrus; HG: Heschl's gyrus; IFG: inferior frontal gyrus; Ins: insular cortex; ITG: inferior temporal gyrus; MFG: medial frontal gyrus; MTG: middle temporal gyrus; Occ: occipital cortex; PHG: parahippocampal gyrus; PostCG: postcentral gyrus; PreCG: precentral gyrus; SF: Sylvian fissure; SMG: supramarginal gyrus; STG: superior temporal gyrus; STS: superior temporal sulcus

Non-montonic tuning to ILD





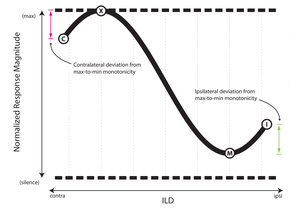
ILD tuning curves plot BOLD response magnitude across ILD values. Leftward ILDs = -30, -20, -10, and -5 dB. Rightward ILDs = 30, 20, 10, and 5 dB Left: tuning curves plotted for individual ROIs. Above: tuning curves plotted for Full AC (all ROIs summed) and for aggregate Posterior (encompassing essentially CM, CL, CPB, A1, and ML) and Anterior regions (RM, RTM, R, AL, RT, RTL, RPB). Blue = LH response. Red = RH response.

- Contralateral bias, but minimum response ar ~10 dB ipsi ILD
- ILD increases monotonically with increasing contra ILD, but does not decrease monotonically with increasing ipsi ILDs

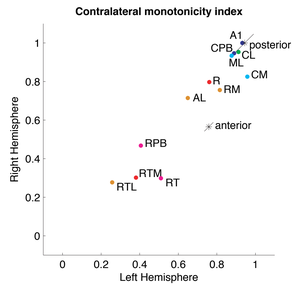
Monotonicity and contralaterality indices

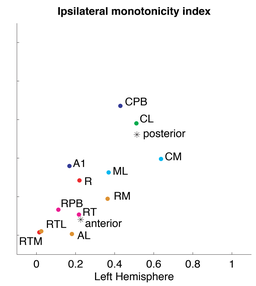
MI contra = X/C
MI ipsi = M/I
CI trad = C - I/C+ I
CI maxmin = C/M (on ipsi side)

Values are derived from mean ROI response relative to response to silence and normalized to max response.



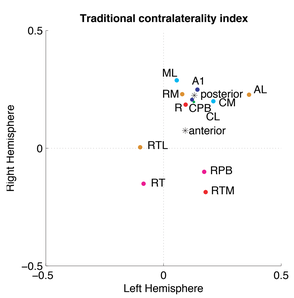
Schematic (left) represents BOLD response to sound varying across ILD:
C = response to max contra ILD
X = max response across ILD values
M = min response across ILD values
I = response to max ipsi ILD

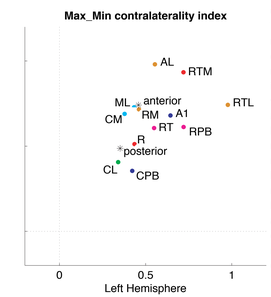




Monotonicity indices (MI): Response to maximum contralateral stimuli (+/- 30 db ILD) relative to overall maximum response (MI contra, far left), and response to maximum ipsilateral stimuli (+/- 30 dB ILD) relative to overall minimum response (MI ipsi, near left). In both figures, MI values for responses in RH are plotted against those in LH. If MI = 1, a monotonic response is indicated. MI < 1 indicates increasing non-monotonicity.

- Response to contra ILD roughly monotonic, especially posterior regions
- Response to ipsi non-monotonic (MI << 1), especially anterior regions

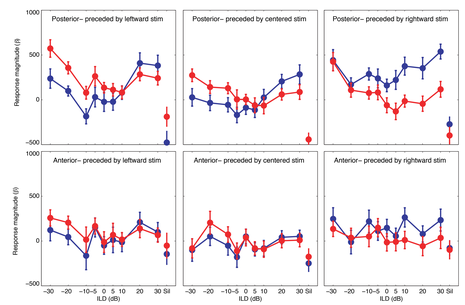




Contralaterality indices (CI). Traditional CI (CI-trad, far left): ratio of response to maximum contra stimuli (+/- 30 db ILD) minus response to maximum ipsi stimuli (+/- 30 dB ILD), divided by the summed responses. Max-Min CI (CI-maxmin, near left): ratio of response to maximum contralateral stimuli minus minimum response to ipsi stimulation, divided by the summed responses. Again, CI values for RH responses are plotted against those in LH. CI > 0 indicates contralaterally biased response, CI < 0 indicates ipsilateral bias. CI = 0 indicates no bias.

- Traditional CI underestimates contralateral bias
- Apparent ipsilateral bias in anterior regions due to non-monotonicity (i.e., ipsi bias not seen with Max-Min CI)

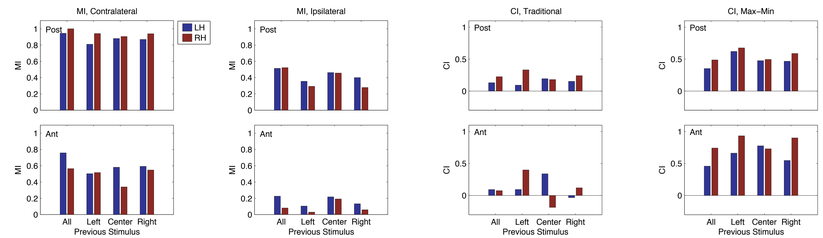
Influence of stimulus-specific adaptation on ILD tuning



ILD adaptation tuning curves (left) for Posterior (upper row) and Anterior (lower row) aggregate ROIs for those trials in which the prior stimulus either favored the left ear (-30, -20, and -10 dB ILD, left column), was centered (-5, 0, 1nd 5 dB ILD, center column), or favored the right ear (30, 20, 10 dB ILD). Blue = LH. Red = RH.

- Overall reduction following ipsilateral stimulus
- Stimulus-specific effects not clear

Influence of stimulus-specific adaptation on monotonicity and contralaterality



Monotonicity and contralaterality indices across adapted states. Indices calculated as in prior analyses. Blue = LH. Red = RH

- Possibly greater non-montonicity (reduced MI ipsi) following lateral (left or right) than central sound, especially in RH.
- Greater contralateral bias following lateral sound (CI Max-Min) suggests adaptation in response to moderate, not large, ILD.

Discussion

- AC fields show contralaterally biased tuning to ILD.

- Traditional CI measures underestimate contralateral bias due to non-monotonic tuning to ILD, especially in anterior regions.

- Greater overall contralateral bias in RH than LH?

- Response to ILD greater in posterior regions and more highly modulated by ILD than response in anterior regions.
- ILD tuning function is more monotonic in posterior than anterior regions.
- Consistent with previously-hypothesized spatial role for posteriorly directed pathways (e.g. Rauschecker & Tian 2000, Arnott et al. 2004).

- Non-monotonicity of ILD ipsilateral tuning possibly due to excitatory contribution of ipsilaterally-tuned neurons (Stecker et al., 2005), or inhibition by ipsilaterally tuned neurons paired with excitation of ipsilateral monaural neurons.

Acknowledgments

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