A comparison of binaural interaction patterns and binaural cue tuning in human auditory cortex

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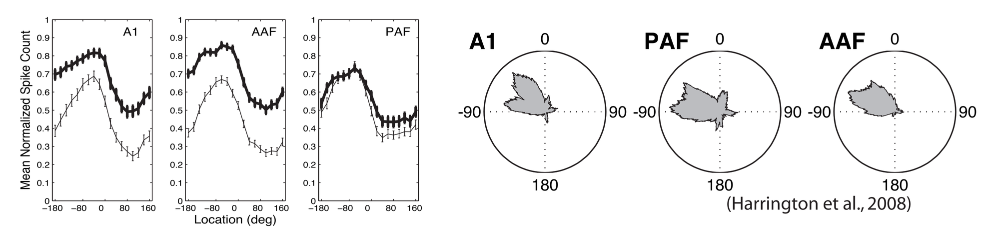
Background: functional MRI evidence for binaural tuning in human auditory cortex (AC)

Contralateral bias for monotic stimuli (Scheffler et al. 1998; Woldorff et al. 1999; Jäncke et al. 2002; Suzuki et al. 2002; Stefanatos et al. 2008). May depend on stimulus context (Schönwiesner et al. 2007).

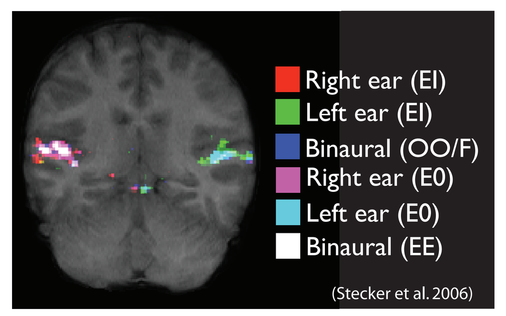
Mixed evidence for facilitation (Scheffler et al. 1998) vs suppression (Jäncke et al. 2002; Stefanatos et al. 2008) with diotic sound.

Mixed evidence for (Krumbholz et al. 2005; von Kriegstein et al. 2008) and against (Zimmer et al. 2006; Woldorff et al. 1999) contralateral bias for sounds carrying binaural cues.

Possible contribution of monaural pathways to contralateral bias for monotic sound (e.g., Stecker et al. 2006)?
Although a majority of AC neurons are binaurally sensitive (Kitzes 2008), many exhibit spatial tuning consistent with monaural gain (e.g., Harrington et al. 2008).



Spatial responses of cat AC neurons strongly favor contralateral locations. Population response (left) and distribution of preferred azimuths (right) reveal contralateral bias, but favored locations coincide with acoustic axis of cat pinnae, suggesting monaural effects.



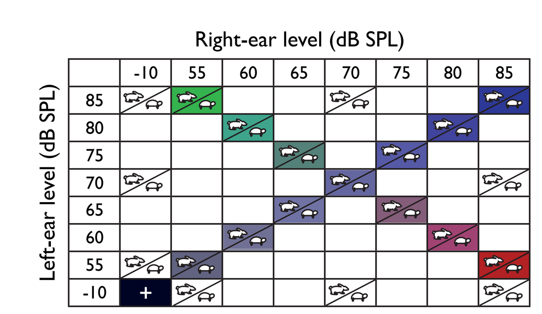
fMRI responses in human AC and inferior colliculus appear dominated by monaural (E0) input. Diotic responses (blue) closely coincide with regions and magnitude of contralateral responses (red for LH, green for RH).

Question: do monotic preferences reflect tuning to binaural cues?

Compare AC responses to monotic sound (single-ear), diotic sound (equal intensity at ears), and sound carrying binaural cues (interaural level difference [ILD]).

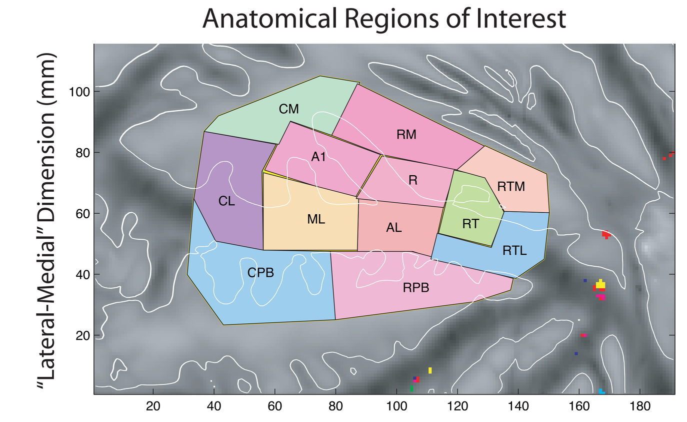
Methods

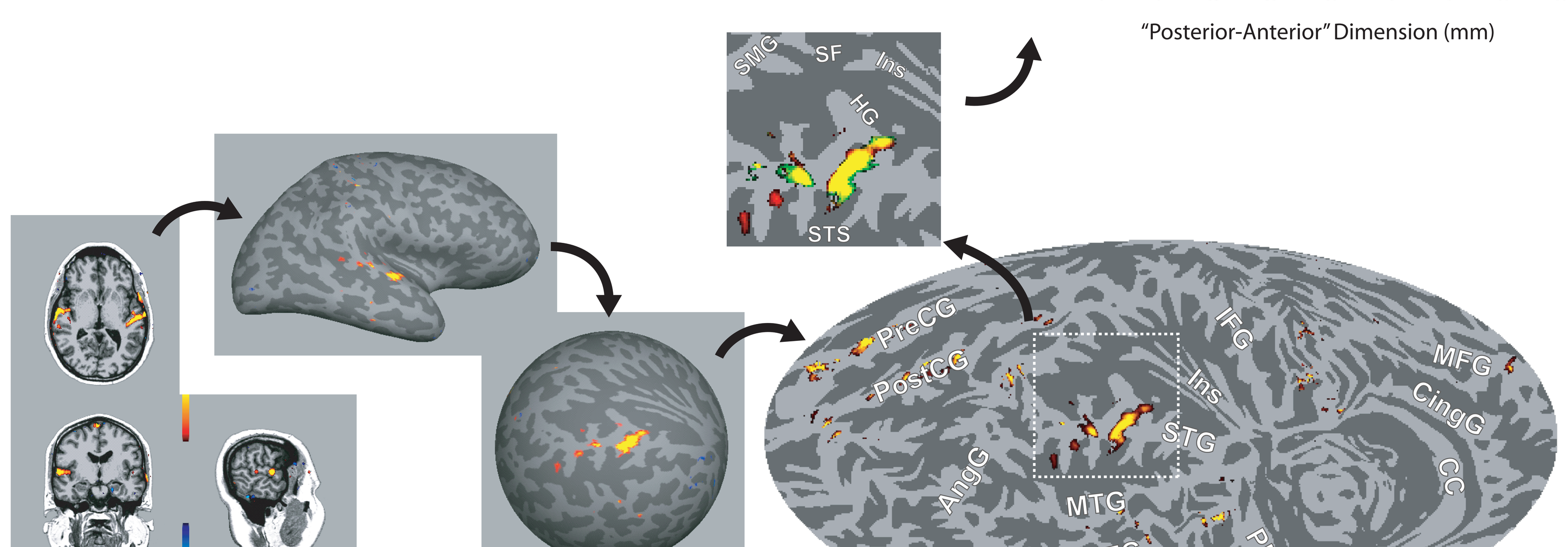
Stimuli	4000 Hz (carrier frequency) Gabor click trains, 3-ms interclick interval (ICI) Presentation rate: 5 trains of 32 clicks ("slow") or 40 trains of 4 clicks ("fast") / sec Level assigned independently at each ear (55-85 dB SPL or silent [-10 dB]) Monotic stimuli presented at 55, 70, and 85 dB SPL Presented via piezo insert earphones (Sensimetrics) in ear defenders
Task	Detect rare (once per ~13s) presentation of 2-ms ICI by button press
Design	12-second blocks present binaural level combination x rate Silent blocks (-10 dB SPL to each ear) occur every 4th block Image acquired at end of each block (sparse acquisition) 3 runs of 57 blocks per subject
Imaging	BOLD echoplanar imaging (Philips, 3 Tesla) Sparse imaging (TR = 12s, one frame per block) 32 slices (4.5 mm), 3mm x 3mm in-plane resolution
Analysis	Resampling to 1x1x1mm (Kang et al. 2007) prior to motion correction 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. *in press* (primate model) ROI response: mean across voxels responding > 50% of maximum sound-silence



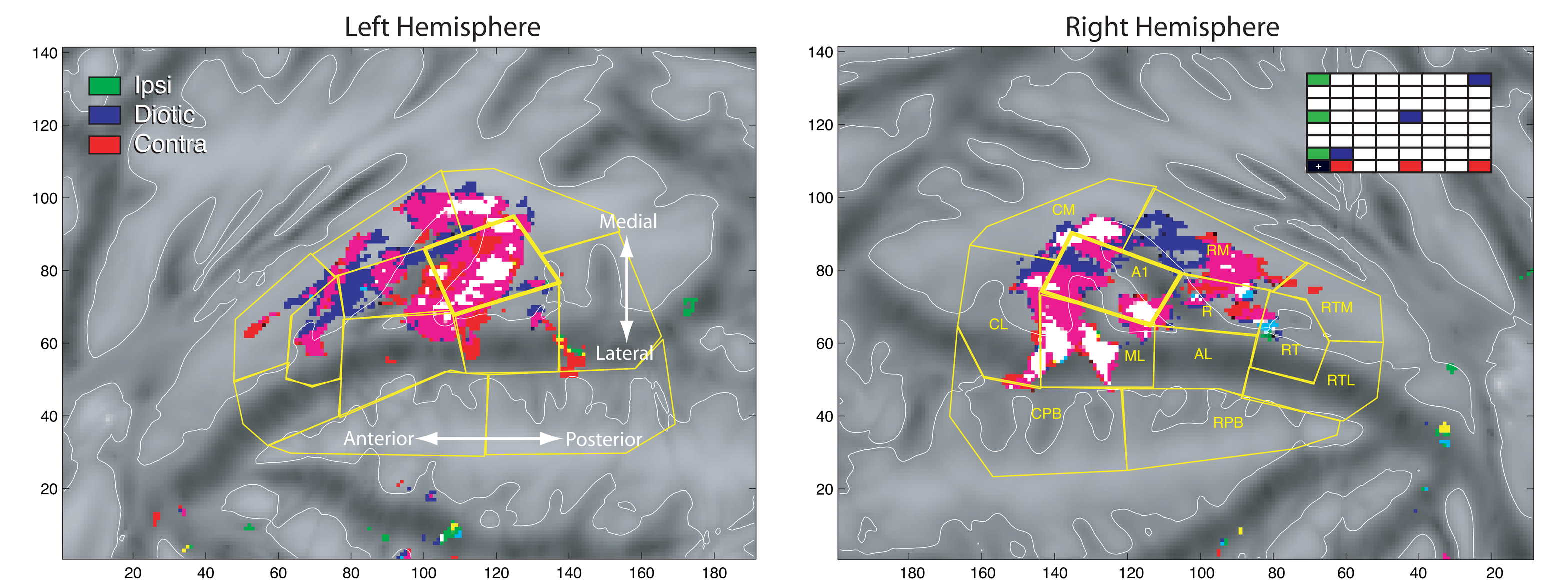
Binaural level combinations presented. Shading illustrates sequences used for testing sensitivity to ABL (shades of blue) and ILD (red to green). Icons (tortoise/hare) represent slow and fast presentation rate. Silent (-10 dB SPL in each ear) blocks indicated by "+".

Anatomical Regions of Interest

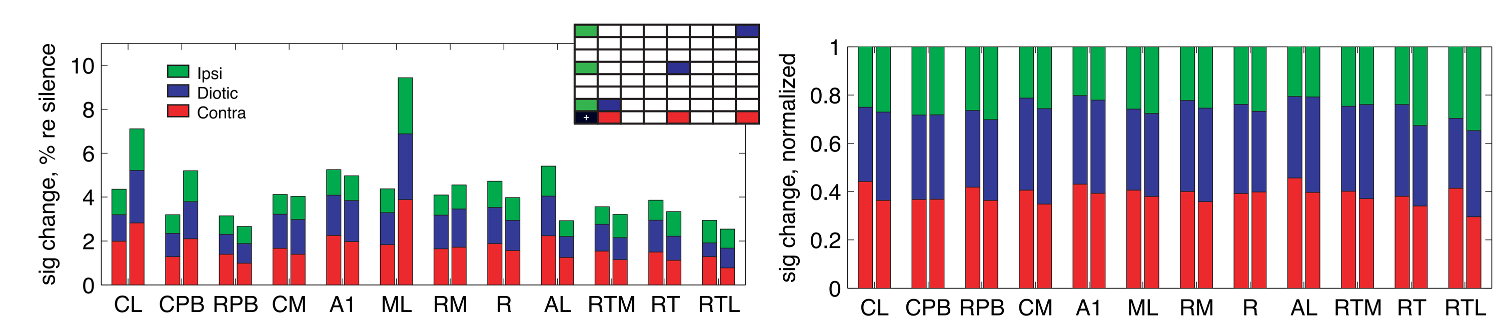




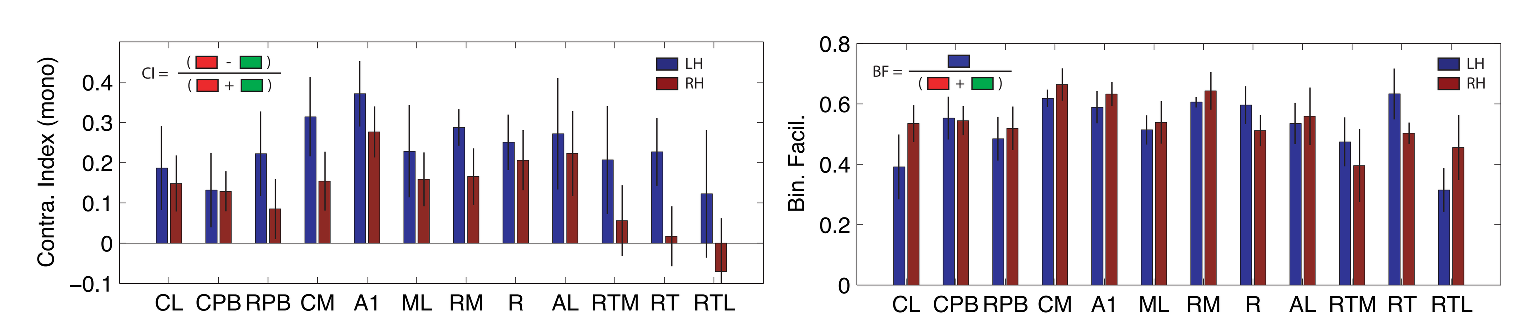
Abbreviations AngG: angular gyrus; CC: corpus callosum; CingG: cingulate gyrus; HG: Heschl's gyrus; IFG: inferior frontal gyrus; Ins: insular cortex; ITG: inferior temporal gyrus; MFG: medial frontal gyrus; MTG: middle temporal gyrus; Occ: occipital cortex; PHG: parahippocampal gyrus; PostCG: postcentral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



Cortical-surface maps illustrate contralateral preference in responses to monotic and diotic sound. Colored shading indicates voxel-wise response greater than 1% signal change (relative to silence), averaged across blocks presenting sound monotically to the contralateral (red), or ipsilateral (green) ear, or diotically (blue). Overlapping activations appear as RGB mixture (magenta, cyan, yellow, white). Activations are averaged across subjects without spatial smoothing, and masked by significant overall response to sound (all conditions combined) relative to silent blocks. Dominant magenta shading in both hemispheres corresponds to contralateral response that is maintained during diotic stimulation ("E0" type). White regions posterior to HG indicate suprathreshold response additionally to ipsilateral sound.

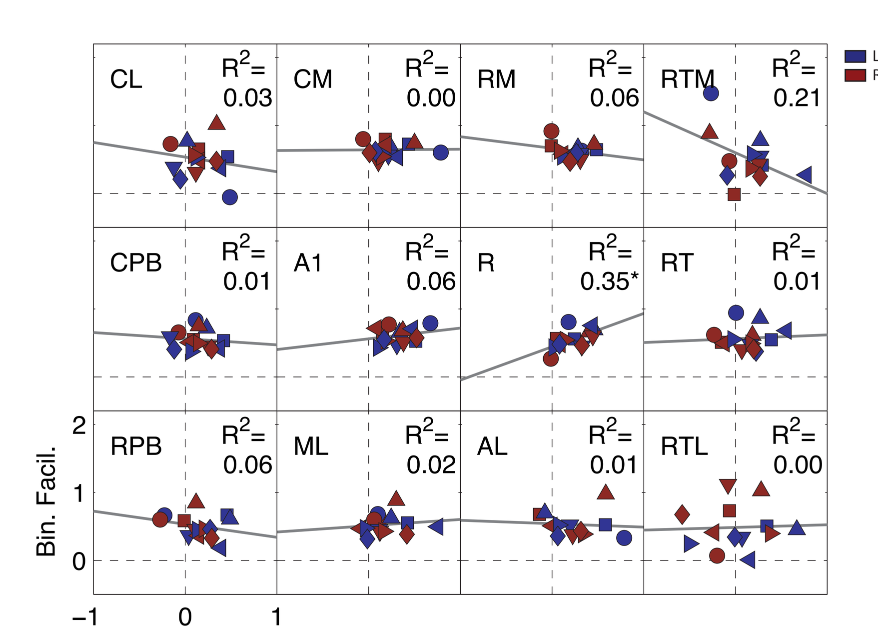


Regional variation in response to monotic and diotic sound reflects mainly differences in overall response magnitude (left panel), modest variation in preference for contralateral stimulation (right panel). Left panel plots overall signal change as a percentage increase above signal measured during silent blocks. Stacked bar elements plot mean responses to contralateral monotic (red), ipsilateral monotic (green) and diotic (blue) stimulation. Left and right bars for each ROI indicate data for left and right hemispheres, respectively. Response magnitude varied by a factor of 2 or more across ROIs, with notable responses observed in right posterolateral AC (regions ML, CL, and CPB). Normalizing by the sum of contralateral, ipsilateral, and diotic responses (right panel) allows a clearer comparison across stimulation types.

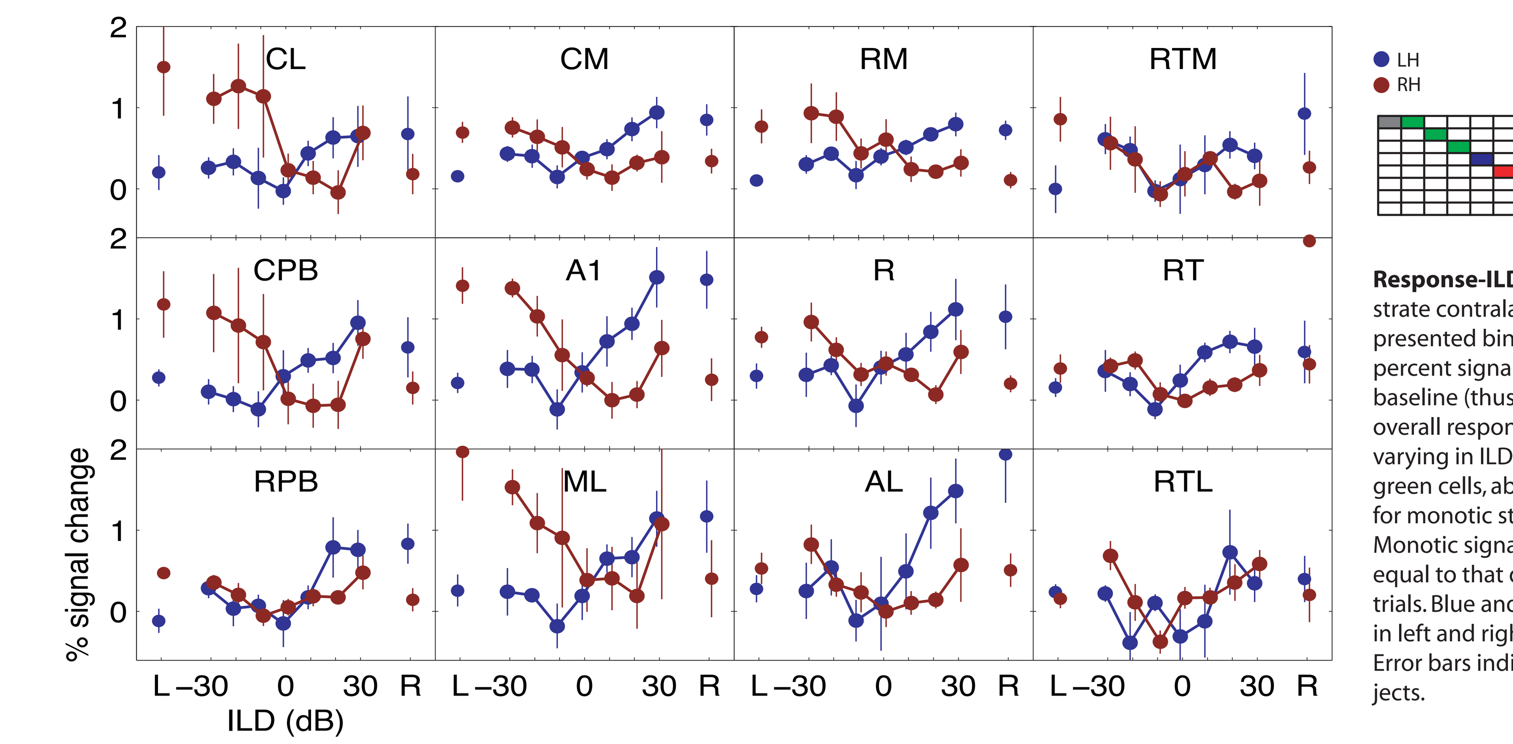


Contralateral preference for monotic stimulation is summarized by the contralaterality index (CI, left panel), computed as the ratio of contralateral minus ipsilateral response to the sum of contralateral and ipsilateral responses. CI ranges from -1 (indicating complete preference for ipsilateral stimulation) through 0 (indicating no preference) to +1 (indicating strong contralateral preference). Plotted across hemispheres and ROIs, CI indicates a consistent preference for contralateral stimulation, except in anterior regions of right AC. Also consistent are modestly larger CI values observed in left than right hemispheres.

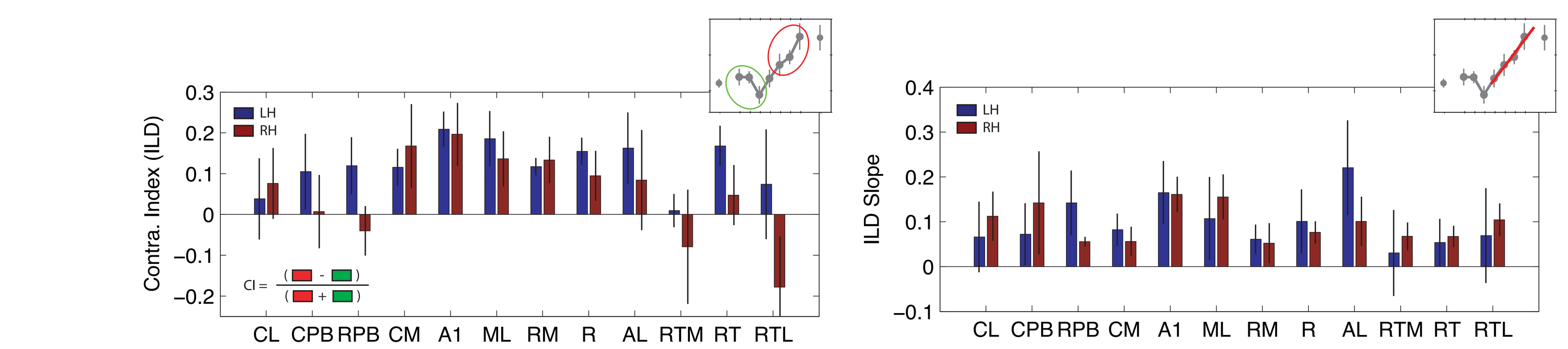
The right panel plots binaural facilitation (BF) index, computed as the ratio of diotic response to the sum of contralateral and ipsilateral responses, across ROIs and hemispheres. A BF value greater than 1 may be taken to indicate facilitation by binaural stimulation (i.e., a response that is greater than expected due to the summation of independent left- and right-ear responses). Observed values fell short of that criterion–averaging approximately 0.5–suggesting diotic responses to be intermediate to contralateral and ipsilateral monotic responses.



Minimal relationship between contralateral preference and binaural facilitation was quantified by linear regression of BF onto CI values across subjects and hemispheres for each ROI. Within each panel, separate symbol types plot values for individual listeners' left-hemisphere (blue symbols) and right-hemisphere (red symbols) responses. Lines indicate regression slopes, and proportion of variance accounted for (R^2) is given for each ROI. Statistically significant regression slopes ($p<.05$) are indicated by asterisk (*).

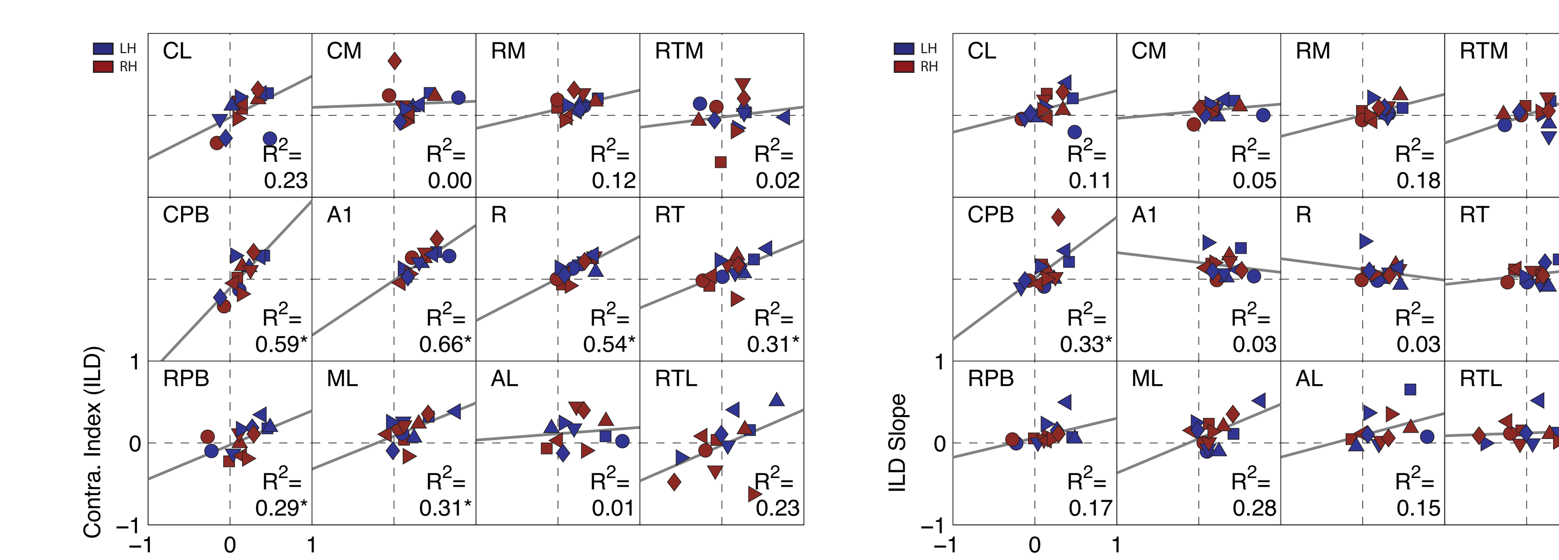


Response-ILD functions (left) demonstrate contralateral preference for stimuli presented binaurally. Each panel plots percent signal change relative to overall baseline (thus normalizing for each ROI's overall response magnitude) for stimuli varying in ILD from -30 to +30 dB (red to green cells, above). "L" and "R" plot values for monotic stimuli (gray cells, above). Monotic signal intensity (85 dB SPL) was equal to that delivered in +/-30 dB ILD trials. Blue and red symbols plot response in left and right hemispheres, respectively. Error bars indicate +/- 1 s.e.m. across subjects.



Contralateral preference of response-ILD functions is summarized by computing contralaterality index (CI, left panel) and response-ILD slope for contralateral ILD values (right panel). CI was computed by first averaging responses to 10, 20, and 30 dB ILD separately for negative (left-favoring) and positive (right-favoring) ILD values. As for monotic analyses, CI was computed as the ratio of contralateral minus ipsilateral response to the sum of contralateral and ipsilateral responses. CI values were computed separately for each combination of subject, ROI, and hemisphere. Bar heights and error bars plot mean CI +/- 1 s.e.m. across subjects. Values greater than 0 indicate contralateral tuning in a majority of ROIs.

ILD slope was computed by fitting a linear regression line to responses for ILD ranging between 0 and 30 dB contralateral, separately for each combination of subject, ROI, and hemisphere. Bar heights plot mean slope +/- 1 s.e.m. aross subjects. Positive slope values indicate that responses increase systematically with increasing contralateral ILD in a majority of ROIs.



Positive correlations between contralaterality measures obtained from response-ILD functions (CI [left panel] and ILD slope [right panel], vertical axes) to measures obtained from monotic responses (CI, horizontal axis) quantify the systematic relationship between contralateral preference and ILD tuning. Correlations were strongest in lateral and posterior regions (e.g., CPB) of the auditory cortex, consistent with suggestions of increasing sensitivity to spatial-cue manipulation along the rostrocaudal axis of the superior temporal plane. In each panel, blue and red symbols plot values measured in left and right hemispheres, respectively, of individual listeners. Lines indicate linear regression slopes; statistically significant correlations ($p<.05$) are indicated by asterisk (*).

Discussion

Consistent with previous reports, most AC fields show a contralateral response preference to monotic sound. As reported by Stefanatos et al. (2008), this effect is greater in the LH than in the RH, and in A1/PAC fields.

No evidence for binaural facilitation in the AC (as in Stefantos et al. 2008; Jäncke et al. 2002), suggestive of the predominance of EI or EO neural populations.

Measures of contralateral bias (e.g., CI) suggest weaker tuning for binaural relative to monotic stimulation. (underestimate?)

Fields in core and lateral/posterior regions show greatest tuning to ILD, highest correlation between monotic & ILD tuning. Consistent with spatial role for posteriorly directed pathways (e.g., Rauschecker & Tian 2000, Arnott et al. 2004).

Acknowledgments

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