# Functional magnetic resonance imaging of binaural cues in human auditory cortex: Non-monotonic response tuning to interaural level difference

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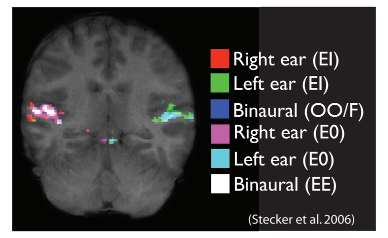
## Functional MRI evidence for binaural tuning in human auditory cortex (AC)

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

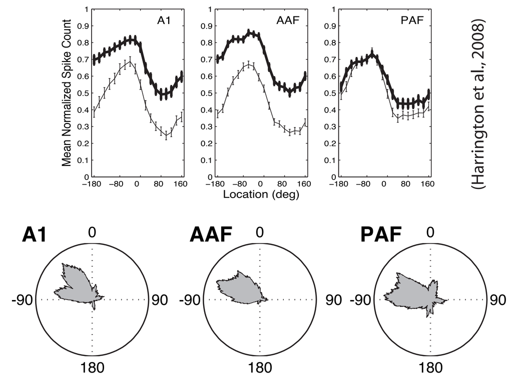
Mixed evidence for (Krumbholz et al. 2005; von Kriegstein et al. 2008) and against (Zimmer et al. 2006; Woldorff et al. 1999) contralateral bias for sounds carrying binaural cues.

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

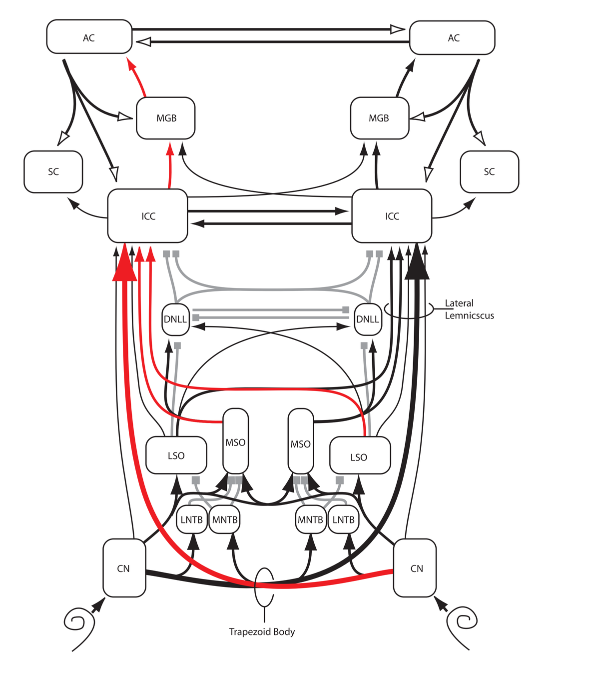
Mixed evidence for facilitation (Scheffler et al. 1998) vs suppression (Jäncke et al. 2002; Stefanatos et al. 2008) with diotic sound.




**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 (e.g., red in LH).




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

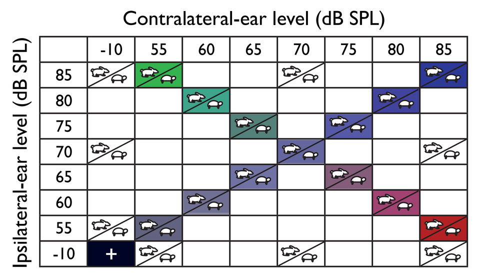


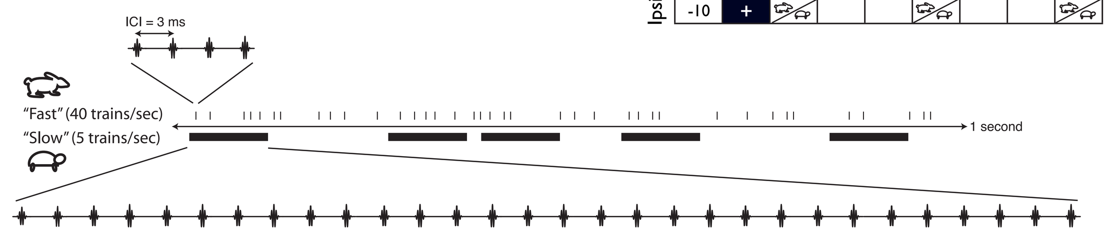

**The ascending auditory pathway** (schematic at left) is dominated by contralateral monaural inputs. Black and red: excitatory inputs; line weights indicate projection magnitudes. Gray: inhibitory projections. Contralateral pathways to left AC highlighted in red for illustration. Major inputs to the inferior colliculus (ICC) include crossed monaural projections from cochlear nucleus (CN) and binaural projections from superior olivary nuclei (LSO & MSO).

## Stimulus & task methods

| | |
|---|---|
| *Subjects* | 7 (5 female) normal-hearing, right-handed subjects |
| *Stimuli* | 4000 Hz (carrier frequency) Gabor click trains, 3-ms interclick interval (ICI)<br>"Slow" (5 trains x 32 clicks/s) or "fast" (40x4 clicks / sec)<br>Independent level at each ear (55-85 dB SPL or silent [-10 dB])<br>Monotic stimuli presented at 55, 70, and 85 dB SPL<br>Piezo insert earphones (Sensimetrics) in ear defenders |
| *Task* | Detect rare (once per ~13s) target (2-ms ICI), indicate by right-hand button press. |

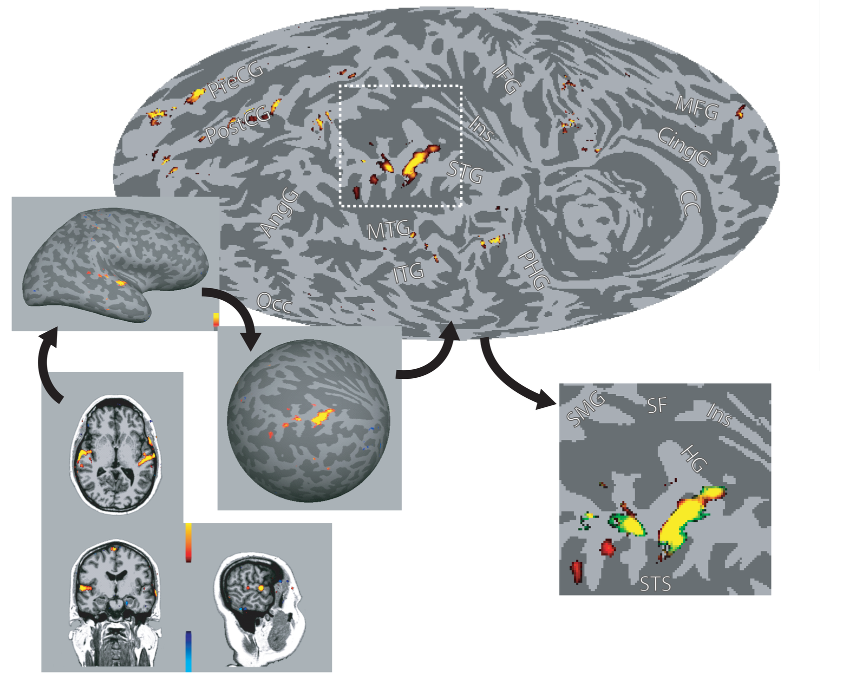
**Right: Binaural level combinations** presented. Shading illustrates sequences used for testing sensitivity to average binaural level (ABL, shades of blue) and interaural level difference (ILD, red to green). Icons (tortoise/hare) represent slow and fast presentation rate. Silent (-10 dB SPL in each ear) blocks indicated by "+".
**Below: Stimulus timecourse.** Each second of stimulation presented 160 narrowband Gabor clicks, grouped into 40 trains of 4 clicks each ("fast" condition) or 5 trains of 32 clicks each ("slow"). Intensity combinations were maintained throughout each 12-second imaging block.



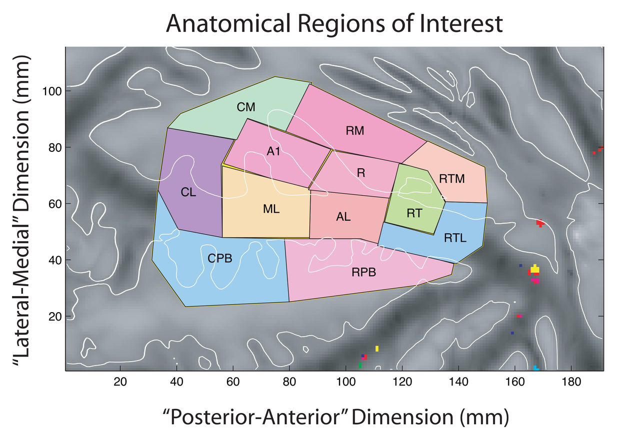




## Imaging methods

| | |
|---|---|
| *Design* | 12-second blocks present binaural level combination x rate<br>Silent blocks (-10 dB SPL to each ear) occur every 4th block<br>Image acquired at end of each block (sparse acquisition)<br>3 runs of 57 blocks per subject |
| *Imaging* | BOLD echoplanar imaging (Philips, 3 Tesla)<br>Sparse imaging (TR = 12s, one frame per block)<br>32 slices (4.5 mm), 3mm x 3mm in-plane resolution |
| *Analysis* | Resampling to 1x1x1mm (Kang et al. 2007) prior to motion correction<br>3D functional preprocessing (motion corr., high-pass filtering [100 s]) in FSL<br>Cortical surface extraction (Freesurfer), spherical alignment between subjects<br>Projection to equal-area map (Mollweide), center on HG x STG, STG on equator<br>12 regions of interest (ROI) according to Woods, et al. 2010 (primate model)<br>ROI response: mean across voxels responding > 50% of maximum sound-silence |



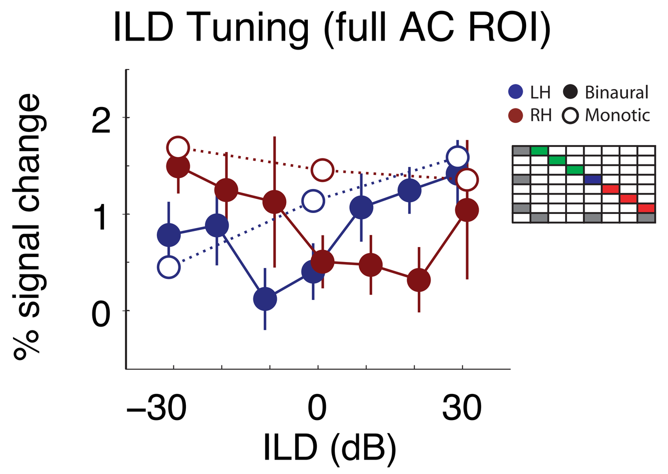

Abbreviations AngG: angular gyrus; CC: corpus callosum; CingG: cingulate gyrus; HG: Heschl's gyrus; IFG: inferior frontal gyrus; Ins: insular cortex; ITG: inferior temporal gyrus; MFG: medial frontal gyrus; MTG: middle temporal gyrus; Occ: occipital cortex; PHG: parahippocampal gyrus; PostCG: postcentral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




**Anatomical regions of interest (ROI)** (right) were defined on the cortical surface following Woods et al. (2010). ROIs are defined on the basis of comparison to functional fields of macaque AC and defined relative to the (spherically aligned) curvature map in human AC. An additional ROI was defined for the entirety of AC (all shaded regions combined).

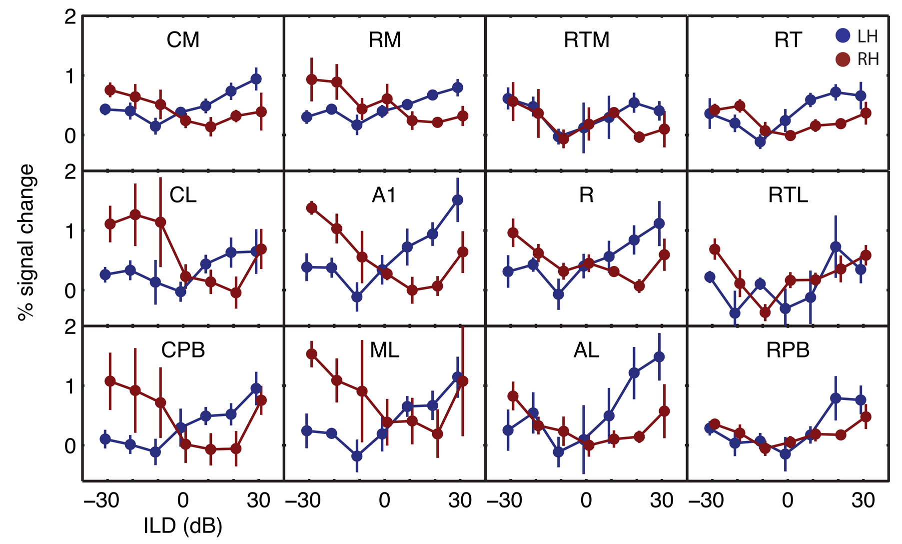
Abbreviations: A1: primary field; AL: anterolateral; CL: caudolateral; CM: caudomedial; CPB: caudal parabelt; ML: mediolateral; R: rostral; RM: rostromedial; RPB: rostral parabelt; RT: rostrotemporal; RTL: rostrotemperolateral; RTM: rostrotemporomedial.

## Non-monotonic ILD tuning of BOLD response: Evidence for binaural suppression in human AC?

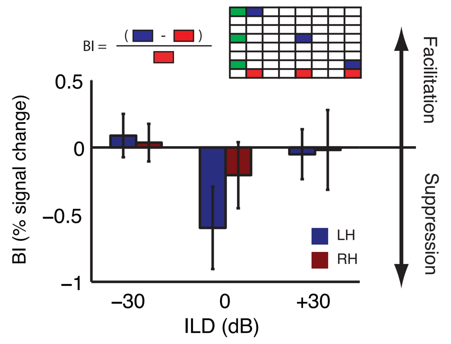



**Response-ILD functions** (left and below) demonstrate contralateral preference for stimuli presented binaurally. Filled symbols plot mean (across subjects) percent signal change relative to overall baseline for stimuli varying in ILD from -30 (louder at left ear) to +30 dB and delivered at an ABL of 70 dB SPL. Error bars plot +/- 1 s.e.m across subjects. Open symbols plot values for contralateral monotic stimuli (gray cells, inset) equated to contralateral ear intensity during corresponding binaural presentations.

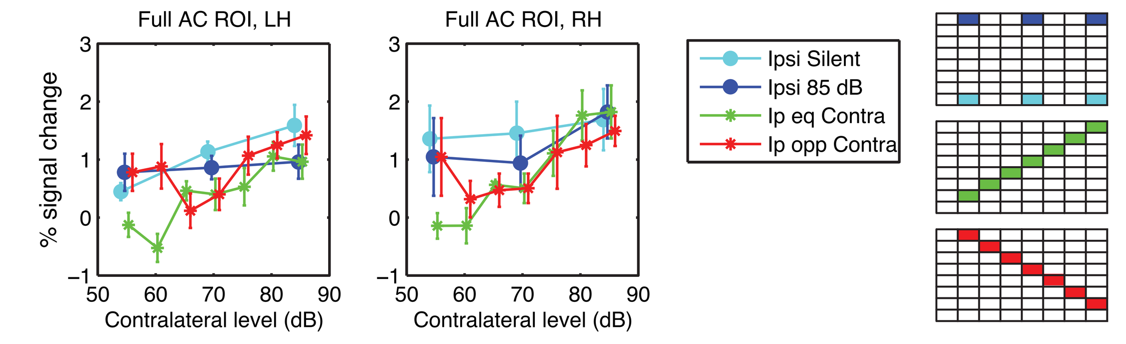
Below: Response-ILD functions for individual ROIs. Formatting as in previous panel.




**Binaural suppression** (right) appears greater for lower intensity-stimuli midline (0 dB) ILD than for extreme left or right-favoring (ILD). Blue and red bars plot magnitude in left and right AC, respectively, averaged across ROIs. Binaural facilitation index (BI) is plotted as the percent signal difference contralateral monotic (red cells in inset panel) and binaural stimuli (blue cells in inset panel), equated in intensity at the contralateral ear. Error bars plot +/- 1 s.e.m. across subjects.




## Excitatory and inhibitory contributions to binaural tuning

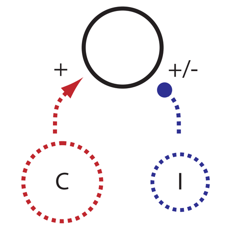


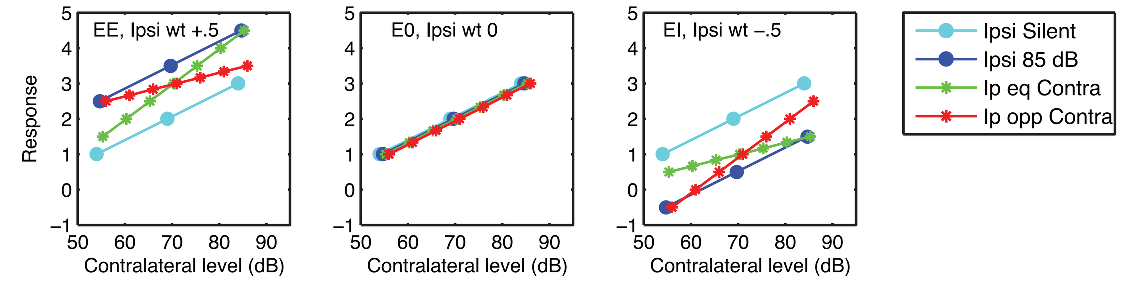

**Response-intensity functions** (above) plot response in percent signal change relative to silent baseline, against intensity level in the contralateral ear. The parameter reflects the intensity level of the ipsilateral ear. Light blue indicate responses to monotic stimulation of the contralateral ear. Dark blue, the response with ipsilateral stimulation constant at the highest tested values (85 dB SPL). Green curves indicate responses to diotic stimulation (equal intensity at the two ears), and red the responses when ipsilateral and contralateral intensities vary in opposition (that is, when ILD is varied with average binaural level held constant). Error bars plot +/-1 s.e.m. across subjects.

**Observations are consistent with ipsilateral inhibition:**
1) Preference for silent vs 85 dB ipsilateral level
2) Preference for monotic over binaural sound
3) Greater response modulation by diotic, ILD stimuli than monotic
4) Non-monotonic ILD tuning (greater inhibition for midline sounds)

## Excitatory vs. opponent contralateral-ipsilateral interactions

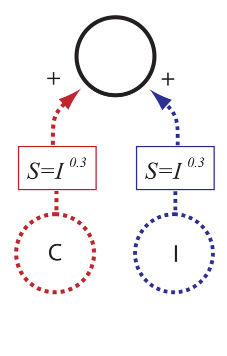
**Binaural interactions** may be characterized according to the type of influence (excitatory or inhibitory) of each ear upon the overall response. Left: a simple characterization of responses as a linear combination of excitation by the contralateral ear and weighted input from the ipsilateral ear. Below: predicted response-intensity functions (see above) for positive (EE, left), zero (E0, center), and negative (EI, right) ipsilateral weighting under the assumption that inputs scale linearly with sound level in dB.



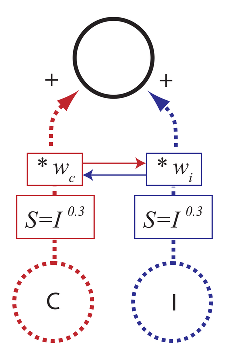

**Comparison to observations**:
1) Steeper response slope for diotic than monotic sound (EE only)
2) Preference for monotic over binaural stimulation (EI only)
3) Not accounted for: Non-monotonic ILD tuning

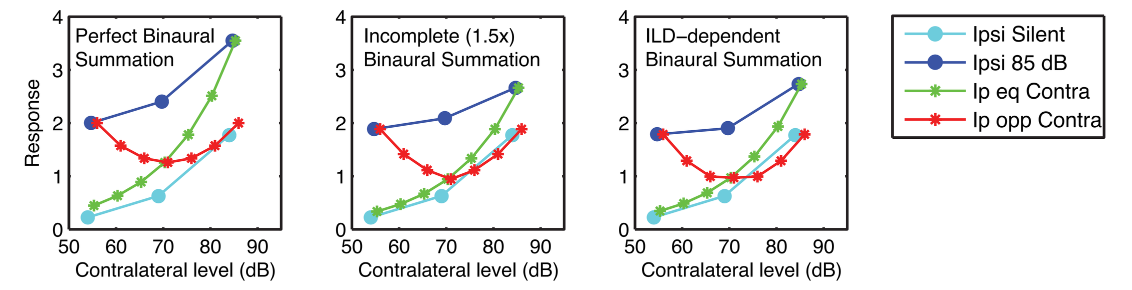
## Contributions of loudness to intensity tuning




**Loudness,** the perceptual correlate of acoustic intensity is affected by many dimensions of a stimulus including its binaural configuration. Right: a model first transforms acoustic intensity at each ear to an estimate of loudness given Stevens' (1957) power law with an exponent of 0.3. The binaural loudness is assumed to be the sum of loudness at the two ears (perfect binaural summation).

Right: a model that includes a weighting factor $w$ for each ear's contribution to central loudness. Incomplete binaural summation, typically around 1.5 times monotic loudness for diotic stimuli is accounted for by reduced contribution ($w$~.5) of the quieter ear. For sounds varying in ILD, Zwicker and Zwicker (1991) measured binaural summation varying from 1.1 (at 20 dB ILD) to 1.54 (0 dB).

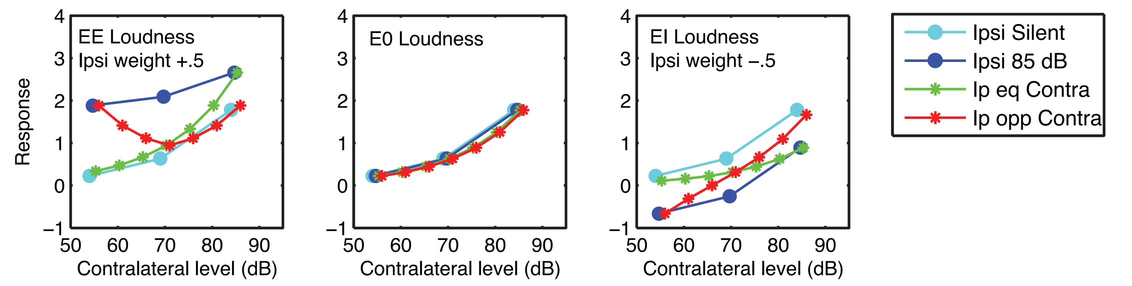



**Predicted response-intensity functions** from binaural loudness models. Left: a model featuring perfect binaural summation. Center: a model featuring incomplete binaural summation, with ear-weighting to give a constant ratio of 1.5 times monotic loudness. Right: a model with ILD-dependent binaural weights, following measurements of Zwicker and Zwicker (1991).

**Comparison to observations:**
1) Non-monotonic ILD tuning due to dominance of the louder ear
2) Steeper slope of diotic intensity tuning compared to monotic
3) Not accounted for: preference for monotic over binaural stimulation (i.e. no inhibition in these EE models)

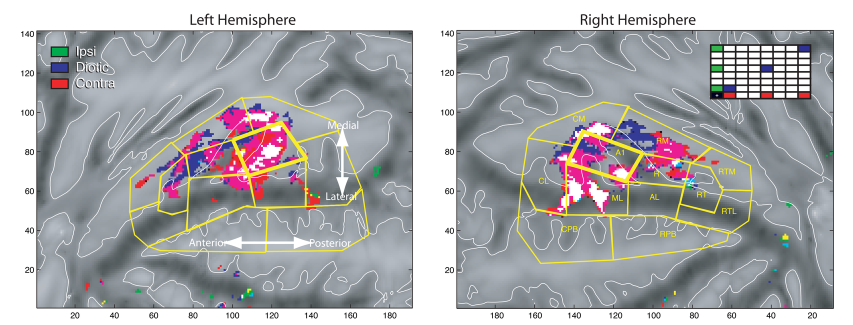
## Combining binaural loudness and ipsilateral inhibition




**Predicted response-intensity functions** from models combining power-law loudness estimation (see above) with ipsilateral input weighted positively (EE, left), negligibly (E0, center), or negatively (EI, right).

**Comparison to observations:**
1) Non-monotonic ILD tuning due to dominance of the louder ear (EE only)
2) Steeper slope of diotic intensity tuning compared to monotic (EE only)
3) Preference for monotic over binaural stimulation (EI only)

## BOLD response maps show contralateral preference for monotic sound




**Cortical-surface maps illustrate contralateral preference** in responses to monotic sound. Left: 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.

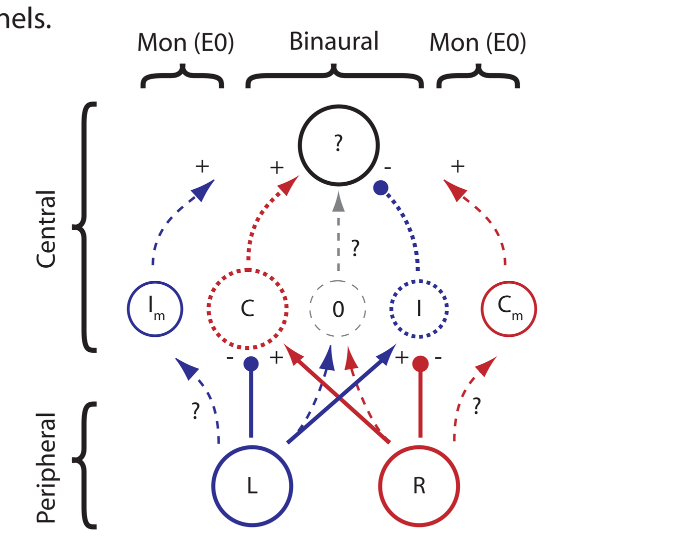
## Summary and Discussion

Human AC response (overall and in most AC fields) shows a **contralateral response preference** to monotic and to dichotic sound, greater in the LH than in the RH, and in A1/PAC fields (Stefanatos et al. 2008).

No evidence for binaural facilitation in the AC (as in Stefanatos et al. 2008; Jäncke et al. 2002). Instead, **binaural suppression** suggests predominance of EI neural populations.

**Non-monotonic ILD tuning** suggests roles of both inhibitory and excitatory ipsilateral populations (Stecker et al. 2005). May reflect two ears' contributions to **central loudness**.

**Spatial coding by hemispatial opponent channels** in each AC has been suggested on the basis of single-unit and psychophysical studies (Stecker et al. 2005, Phillips 2008, Wise & Irvine 1985). Current results suggest additional excitation by monaural channels.




Expanded opponent-channel architecture includes possible contributions of monaural ($I_m$, $C_m$) and midline (0) channels.

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