Monaural and binaural contributions to spatial cue tuning in human auditory cortex

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A31

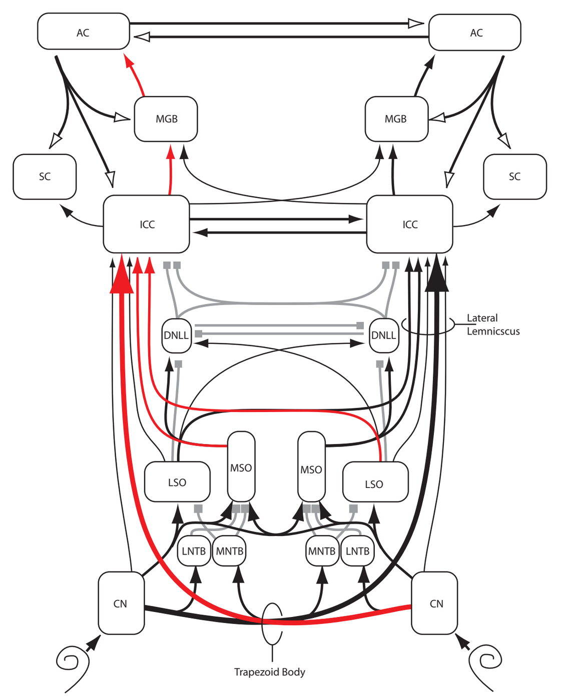
Functional MRI evidence for binaural tuning in human auditory cortex (AC)

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).

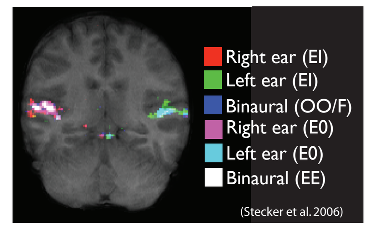
Mixed evidence for (Krumbholz et al. 2005; von Kriegstein et al. 2008) and against (Zimmer et al. 2006; Woldorff et al. 1999) contralateral bias for sounds carrying binaural cues.

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).

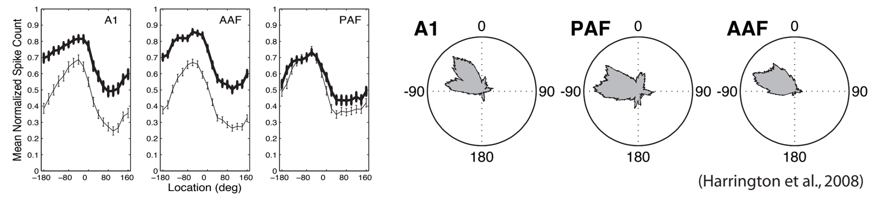
Mixed evidence for facilitation (Scheffler et al. 1998) vs suppression (Jäncke et al. 2002; Stefanatos et al. 2008) with diotic sound.



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).



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).

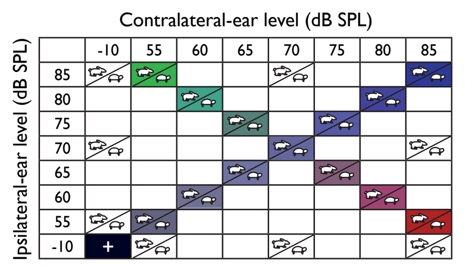


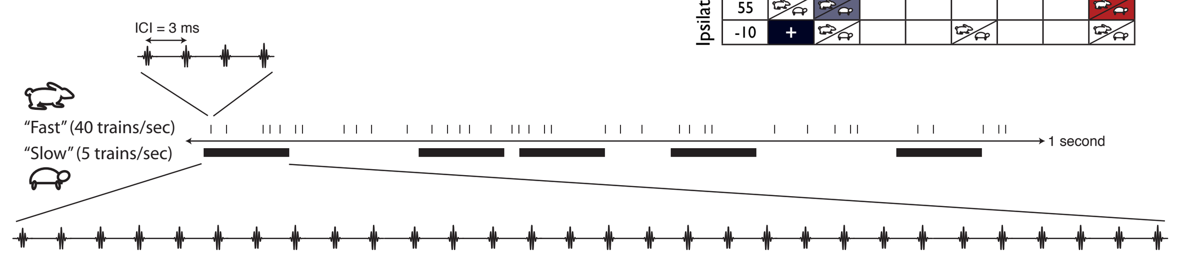
Spatial responses of cat AC neurons strongly favor contralateral locations. Population response (left) and distribution of preferred azimuths (right) reveal contralateral bias, but favored locations coincide with acoustic axis of cat pinnae, suggesting monaural effects.

Stimulus & task methods

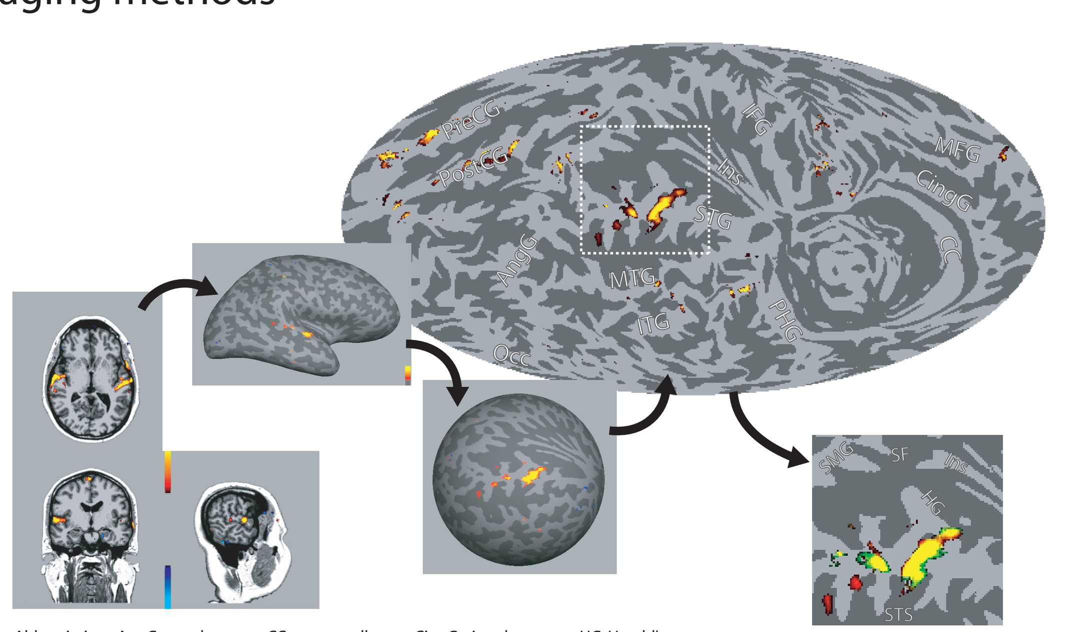
Subjects	7 (5 female) normal-hearing, right-handed subjects
Stimuli	4000 Hz (carrier frequency) Gabor click trains, 3-ms interclick interval (ICI) Presentation rate: 5 trains of 32 clicks ("slow") or 40 trains of 4 clicks ("fast") / sec Level assigned independently at each ear (55-85 dB SPL or silent [-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

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.





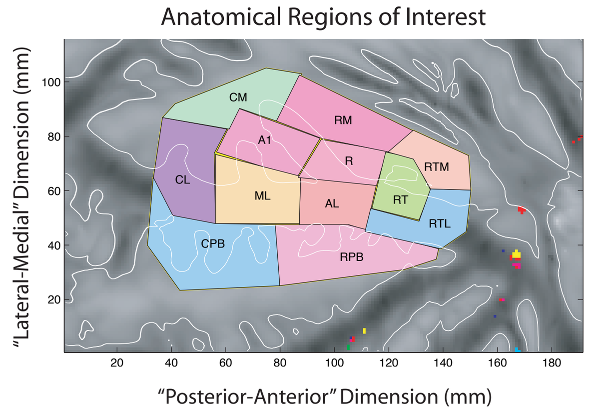
Imaging methods



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

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. 2010 (primate model) ROI response: mean across voxels responding > 50% of maximum sound-silence

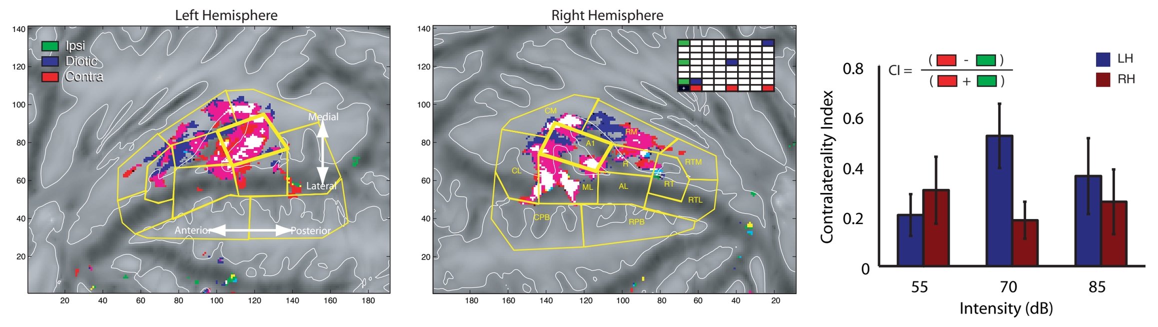
Anatomical Regions of Interest



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).

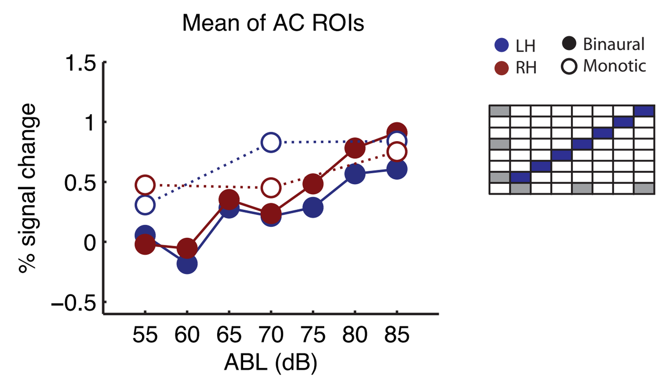
Abbreviations: A1: primary field; AL: anterolateral; CL: caudolateral; CM: caudomedial; CPB: caudal parabelt; ML: mediolateral; R: rostral; RM: rostromedial; RPB: rostral parabelt; RT: rostrotemporal; RTL: rostrotemperolateral; RTM: rostrotemporomedial.

BOLD response maps reveal contralateral preference for monotic sound



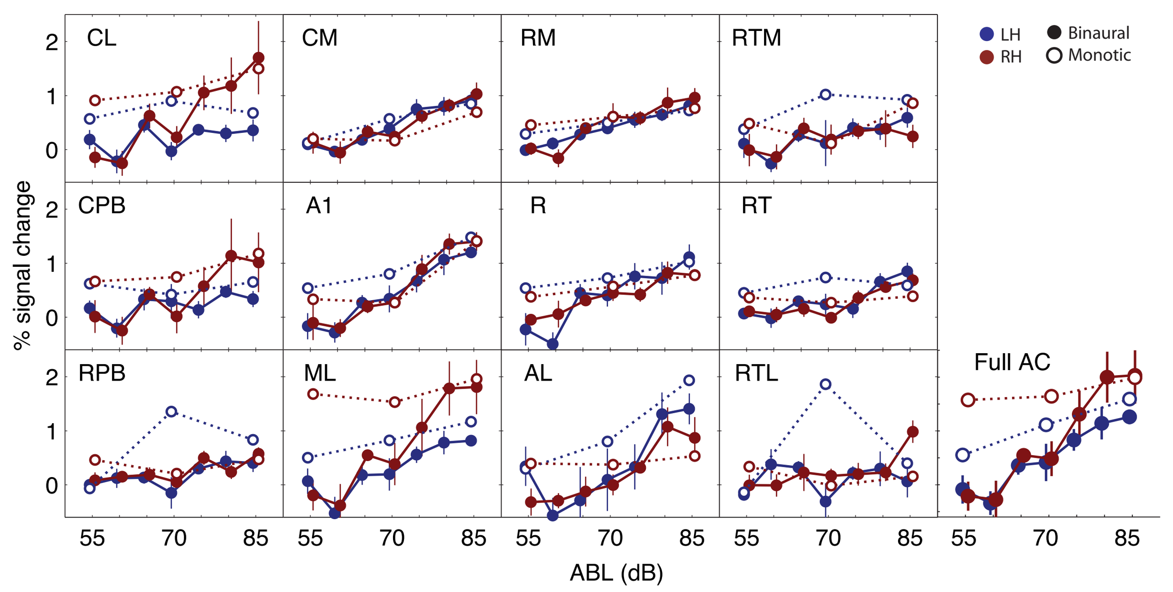
Cortical-surface maps illustrate contralateral preference in responses to monotic sound. Left: colored shading indicates voxel-wise response greater than 1% signal change (relative to silence), averaged across blocks presenting sound monotically to the contralateral (red), or ipsilateral (green) ear, 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. Right: contralaterality index (contra-ipsi difference normalized by sum) averaged across AC ROIs demonstrates contralateral preference (CI>0), slightly greater overall in the left than right hemisphere and at moderate (70 dB) intensity.

Response-intensity functions reveal binaural suppression at low intensities

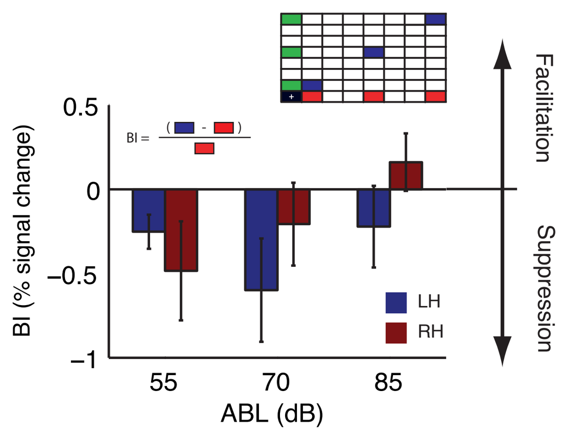


Response-intensity functions (above) plot percent signal change relative to overall baseline against average binaural level (ABL) for sounds presented diotically (filled symbols) or monotically to the contralateral ear (open symbols). Individual ROIs were separately baselined prior to averaging. Roughly monotonic increases with ABL, as described by Sigalovsky & Melcher (2006), were observed in both hemispheres (blue: LH, red: RH) Steeper slopes are apparent for binaural than monaural presentation. That is, binaural responses were reduced compared to monaural responses, at low intensities. At higher intensities, binaural and monaural responses were more similar.

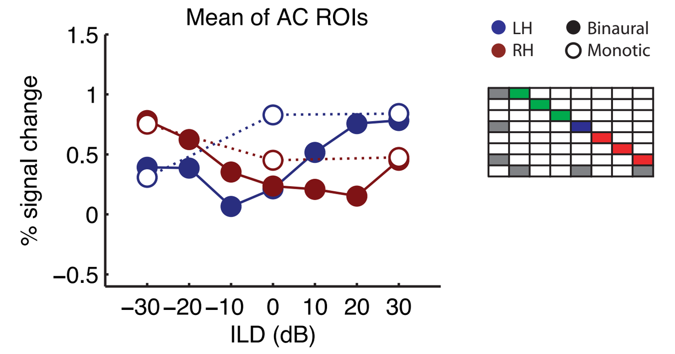
Below: response-intensity functions for individual ROIs. Error bars indicate +/- 1 s.e.m. across subjects. Other formatting as above.



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.

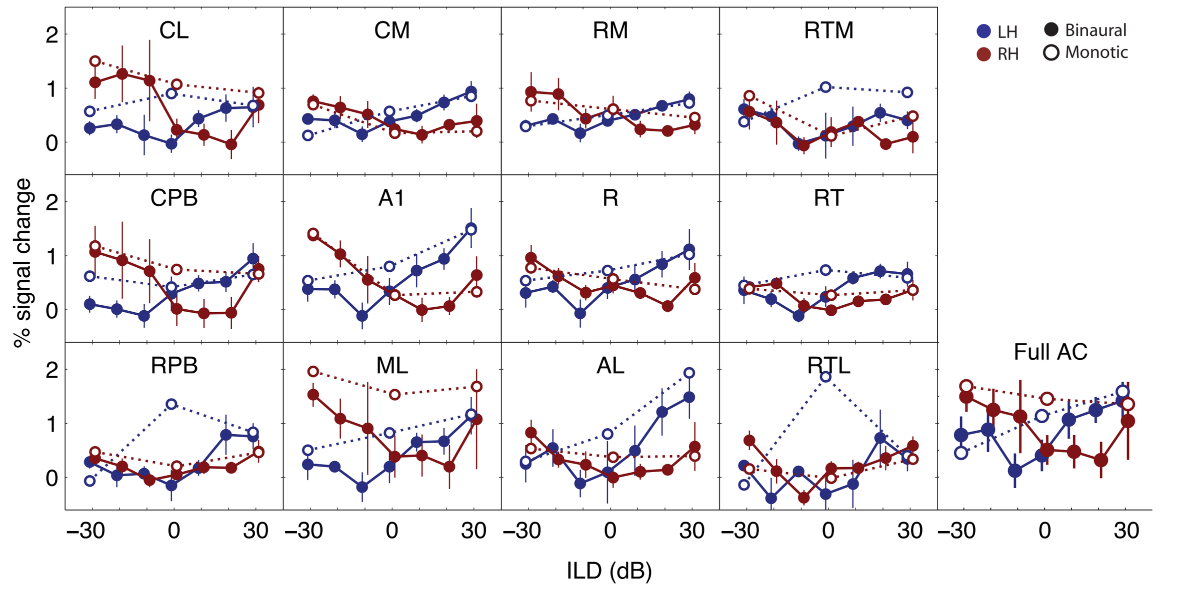


Binaural suppression shapes tuning to interaural level difference (ILD)

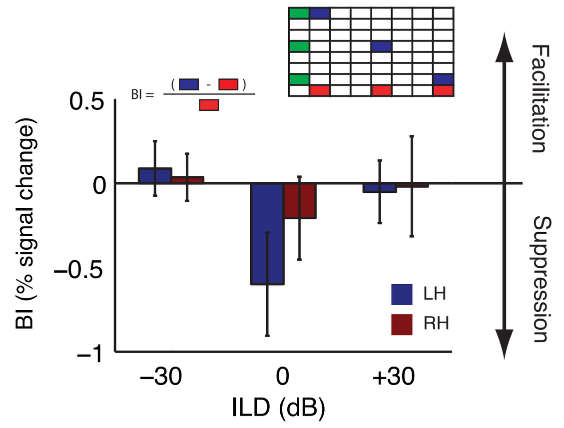


Response-ILD functions (above) demonstrate contralateral preference for stimuli presented binaurally. Filled symbols plot percent signal change relative to overall baseline for stimuli varying in ILD from -30 (louder at left ear) to +30 dB and delivered at an ABL of 70 dB SPL. Open symbols plot values for contralateral monotic stimuli (gray cells, above) equated to contralateral ear intensity during corresponding binaural presentations. Baselining, averaging, and plot formatting as in previous panel.

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



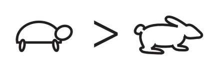
Binaural suppression (right) appears greater for midline (0 dB) ILD than for extreme left or right-favoring ILD. Blue and red bars plot binaural facilitation index BI (see previous panel) in left and right AC, respectively, averaged across ROIs and plotted against ILD.



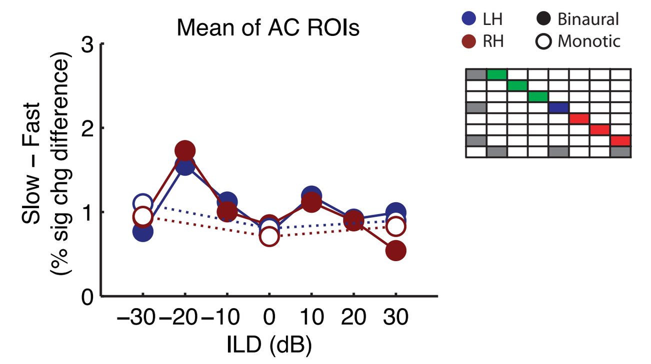
Rate-dependent response adaptation is ILD-dependent

Reduced AC response to stimulus repetition compared to novel stimulus (stimulus-specific adaptation; Ulanovsky et al. 2003).

AC BOLD responses depend on presentation rate: *sustained response* diminishes with rate from 2/s -> 35/s (Harms & Melcher 2002).

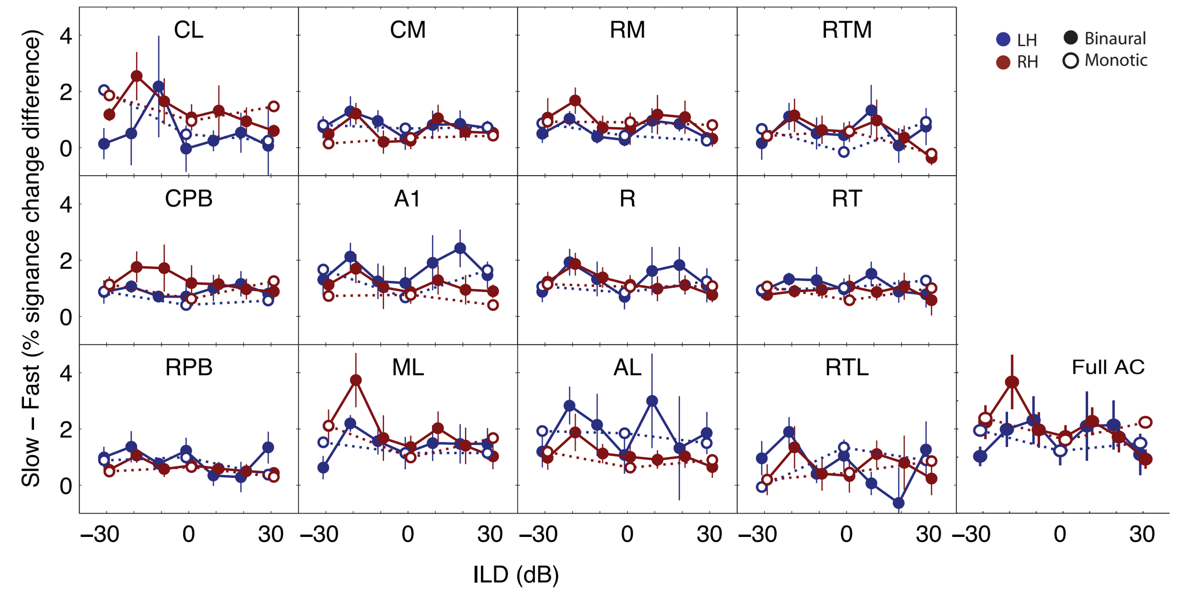


Hypothesis: responses during "fast" presentation (40/s) will be reduced compared to "slow" presentation (5/s).



Effects of stimulus presentation rate are quantified above as the difference in response magnitude (percent signal change) across stimulus presentation rates. The presentation-rate effect is positive overall, corresponding to greater activation for slow than fast presentations (cf. Harms & Melcher 2002). Plotted against ILD, the effect appears greatest for moderate ILD values of 10-20 dB contralateral or ipsilateral. The effect appears reduced for small (0) or large (+/- 30 dB) ILD values. Symbols, colors as in previous panels.

Below: rate-effect functions for individual ROIs. Presentation-rate effect calculated as described above. Plot formatting as in previous panels.



Summary

Consistent with previous reports, most AC fields show a **contralateral response preference** to monotic 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 Stefantos et al. 2008; Jäncke et al. 2002). Instead, **binaural suppression** suggests predominance of EI neural populations.

Clear modulation of response by presentation rate (Harms & Melcher 2002). **Response adaptation** apears greatest for moderate ILD values.

Hemispheric asymmetry in response adaptation: contralateral in RH, bilateral in LH (Salminen et al. 2010).

Stronger ILD tuning in core and lateral/posterior regions, consistent with **posterior "where" pathway** (e.g., Rauschecker & Tian 2000, Arnott et al. 2004).

Opponent-channel theory of AC spatial coding

Spatial coding by hemispatial opponent channels in each AC (Stecker et al. 2005, Phillips 2008, Wise & Irvine 1985).

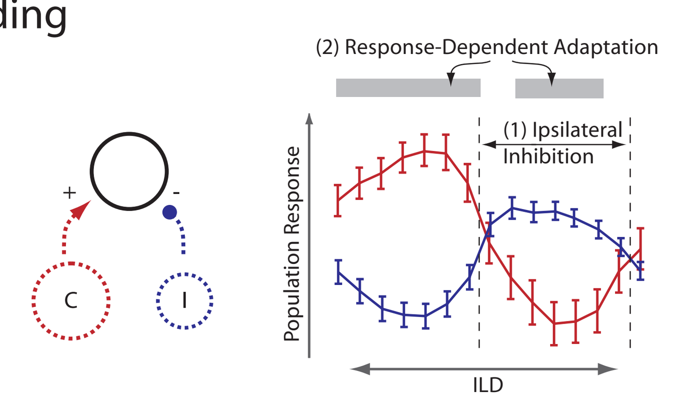
With respect to current results:

(1) Binaural suppression due to inhibition by ipsilateral input.

(2) Rate-dependent adaptation greatest for ILDs driving strong responses of at least one channel. Unkown whether adaptation affects inputs or channel responses.

(3) Similar monaural and large-ILD responses: role of monaural or EI pathways?

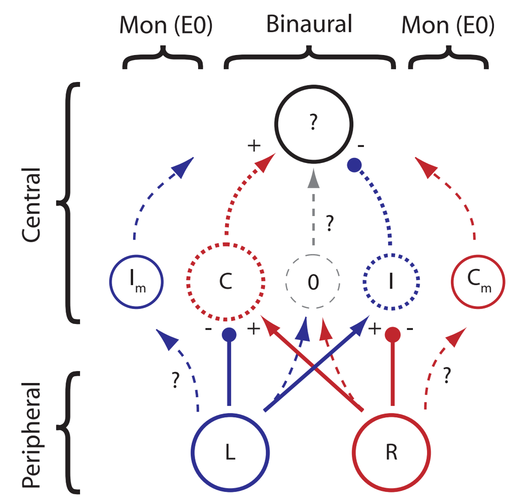
(4) Contribution of midline channel (Dingle et al. 2010)?



Above left: conceptual architecture of neural populations representing contralateral and ipsilateral opponent channels within left AC (Stecker et al. 2005).

Above right: hypothetical responses of contralateral (red) and ipsilateral (blue) channels (adapted from Harrington et al. 2008). Note the unequal channel responses, consistent with smaller population of AC neurons tuned to ipsilateral ILD.

Left: expanded architecture includes possible contributions of monaural (I_m, C_m) and midline (0) channels.



Acknowledgments

MR technical support:
Jeff Stevenson and Jenee O'Brien.

SPACElab: Andrew Brown, Julie Stecker, Sofia Penev.

Funding support: NSF IOB-0630338, NIH R03 DC009482-02S1, NIH T32 DC005361.

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