Cortical and sub-cortical mechanisms of binaural pitch processing: Evidence from MEG

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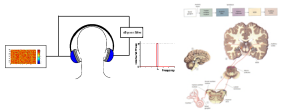
Introduction

Huggins Pitch (HP) is a dichotic pitch stimulus that is generated by presenting a random noise signal to one ear, and the same noise with a phase shift over a narrow frequency band to the other ear (Cramer & Huggins, 1958). The percept is that of a faint tonal object (corresponding to the center frequency of the phase shifted band) embedded in noise.

Huggins Pitch generation:



What is intriguing about this phenomenon is that the input to either ear alone is just white noise with no spectral or temporal cues to pitch. The fact that we are able to perceive the pitch indicates that it is created by a central mechanism that receives the inputs from the two ears, computes their commonalities and differences and then translates these into a tonal percept.

Here we compare the cortical auditory evoked responses to HP with those of tones embedded in noise (TN). These perceptually similar but physically very different stimuli are interesting tools for the study of the electrophysiological correlates of auditory processing in cortex. Furthermore, they enable us to examine the mechanisms behind the widely encountered but poorly understood auditory cortical onset responses such as the M100.

Experiment 1 (N=20)

Stimuli

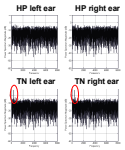
9 conditions (random presentation)

- **Control condition (800 trials):** 1500 ms of interaurally correlated white noise
- **Pitch condition (8x100 trials):** 1000 ms of correlated noise continued by either
  - 500 ms of HP (with center frequencies of 200Hz, 400Hz 600Hz 1000Hz)
  - 500 ms of Pure Tone embedded in noise (same frequencies)

All stimuli were ramped on and off with 15 ms cosine squared ramps (no ramp at pitch onset), had similar power spectral densities and matched perceived tone loudness.

Signals presented at approx 75dB SPL and adjusted according to each subject's perception of HP lateralization.

Stimuli example: Power Spectral Density estimate of the 400 Hz stimuli.



Procedure

Subjects performed a pitch detection task (50% of trials).

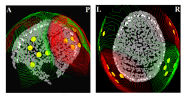
Auditory cortical responses were recorded using a 160 channel whole head MEG system (KIT, Kanazawa, Japan).

Signals were delivered with Etymotic ER3-A insert earphones.

All subjects were right-handed, with normal hearing and no known neurological disorders.

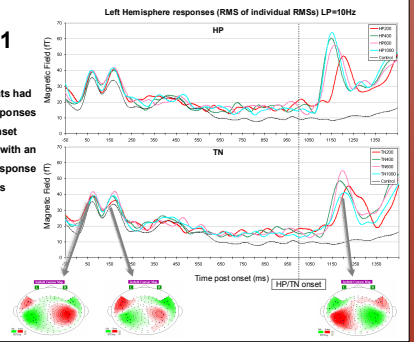
Channel selection:

5 most active channels in each sink and source of the pre-test M100 response were selected for further analysis



Results Experiment 1

Waveform analysis reveals that all participants had comparable response trajectories. These responses were characterized by a two-peaked noise onset response at ~70ms and ~160 ms post onset (with an M50 spatial distribution) and a pitch onset response (with an M100 spatial distribution) at ~1160ms modulated by perceived pitch.

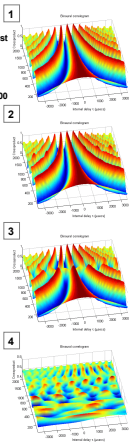


(Contour data from a representative subject)

Model

Neurons in the Superior Olivary Complex (SOC) are the first point in the ascending auditory pathway that exhibits binaural interaction. Cells in the Medial Superior Olive (MSO) are believed to function as coincidence detectors. The MSO is generally modeled as a two dimensional matrix of cells arranged according to best interaural delay and characteristic frequency (CF).

1. Model of MSO activation for interaurally correlated white noise (first 1000 of all stimuli). Some cells (with best interaural delay of 0 ms and 1/cf) are highly active (ridges). Other cells are inactive (valleys)
2. Model of MSO activation for 1000Hz TN. Activation pattern is very similar to (1) except that there is added activation on the peaks that correspond to 1000Hz. (some cells that were already active in the preceding 1000 ms become slightly more active when TN turns on)
3. Model of MSO activation for 1000Hz HP. Some cells that were inactive in the first 1000ms of the stimulus (in the valleys) are activated with pitch onset.



This differential activation of the MSO might explain the results observed in experiment 1 - HP stimuli activated cells that were not previously active and thus responded more quickly.

4. We change the initial 1000 ms of all stimuli so that the correlated noise is replaces by an interaurally uncorrelated signal.

Predictions:

- Response to HP in Experiment 2 will be later than in Experiment 1
- Response to TN in Experiment 2 will be earlier than in Experiment 1
- Responses in Experiment 2 will be noisier than Experiment 1

Neural transduction model – half wave rectification

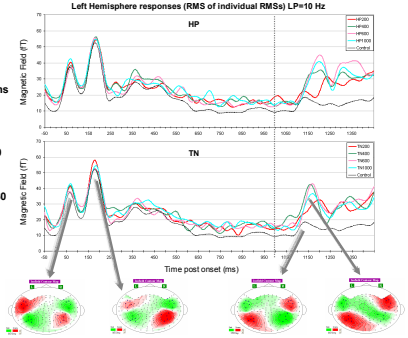
Plots generated with "Binaural Tool Box" by Michael Akeroyd (2001).

Results Experiment 2 (N=16)

First 1000ms of all stimuli are replaced by interaurally uncorrelated white noise.
Two changes occur simultaneously at 1000 ms post onset:

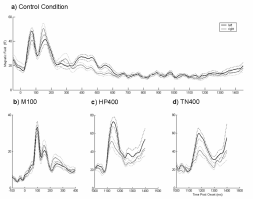
1) change in noise (from uncorrelated to correlated) that is reflected in a peak at ~1140 ms in the control condition.

2) onset of pitch – reflected in a peak at ~1160 ms, modulated by perceived pitch.



(Contour data from a representative subject)

Hemispheric Differences:



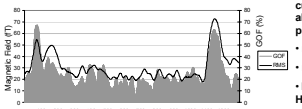
In Experiment 1, pitch onset responses for both TN and HP were stronger in the *Left Hemisphere*.

The noise onset responses also showed hemispheric differences with M50 stronger on the left hemisphere and M150 stronger on the right hemisphere, but these were weaker effects.

In Experiment 2, the response that corresponds to the change in noise is stronger in the *right hemisphere*

The figure shows responses for 400 Hz stimuli as an example. The effect was seen in all stimuli

The Location of the Source of the Pitch Onset Response

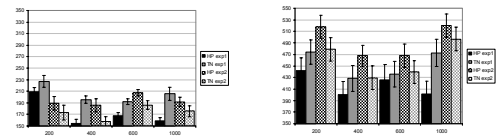


The proportion of the Pitch onset response field (HP400, LH) explained by the current dipole obtained for the M50 components (Average across 13 listeners)

The goodness of fit (GOF) of the M50 dipole (single equivalent current dipole), maintaining a fixed location and orientation but allowing for a 180 degree flip in polarity, was estimated for the pitch onset component in HP400 and TN400.

- mean GOF for M50 =88.77% (std=4.3)
- mean GOF for Pitch Onset Response = 77.3% (std =12.52)
- M50 component originates in the antero-lateral portion of Heschl's gyri and Heschl's sulcus (Yvert et al, 2001)
- the good fit suggests that the sources of the activity lie in close proximity in auditory cortex, perhaps on opposite sides of a cortical fold.

Comparing Experiment 1 and Experiment 2



Behavior

- Overall, response time is longer in Experiment 2 than in Experiment 1 (task is harder)
- Faster responses to HP in Experiment 1, and TN in Experiment 2

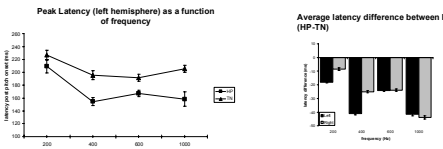
Electrophysiology

- Overall, fastest response is to HP in Experiment 1, and slowest response is to TN in Experiment 1 (as predicted)

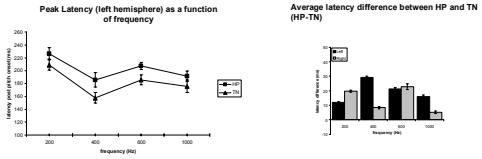
Conclusions

- The 1000 ms preceding the onset of HP/TN have a critical effect on the response for that stimulus.
- The data supports the suggested model of binaural interaction.
- Explanations of the M100 response latency that refer to cochlear effects (for example, Greenberg et al 1998) must be reconsidered.
- Cortical responses approx 160 ms post pitch onset provide qualitatively different information than behavior.
- Findings enable the investigation of cortical expansion of latency disparities.

Results Experiment 1 - peak latencies are significantly earlier for HP trials.



Results Experiment 2 - peak latencies are significantly later for HP trials.



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Yvert, B., Crouzeix, A., Bertrand, O., Seither-Preisler, A., and Pantev,C. 2001. Multiple supratemporal sources of magnetic and electric auditory evoked middle latency components in humans. *Cereb. Cortex* 11: 411–423.

Acknowledgements

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