Neural Rhythm Synchronizes With Imagined Acoustic Rhythm

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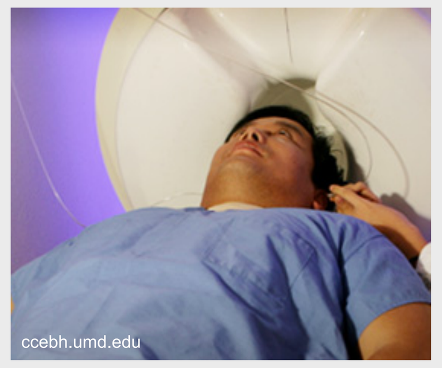
Introduction

Cortex is thought to generate internal models of incomplete sensory data, but the mechanisms are yet unresolved. One possibility is contextual interpolation, such as in perceptual filling-in illusions.

In response to rhythmic sounds, auditory cortex track target rhythms as a steady-state response (**aSSR**) [1]. We analyze aSSR disruptions following noise interruptions to rhythmic sound, in order to examine these disruptions when listeners incorrectly perceive an absent target rhythm in noise.

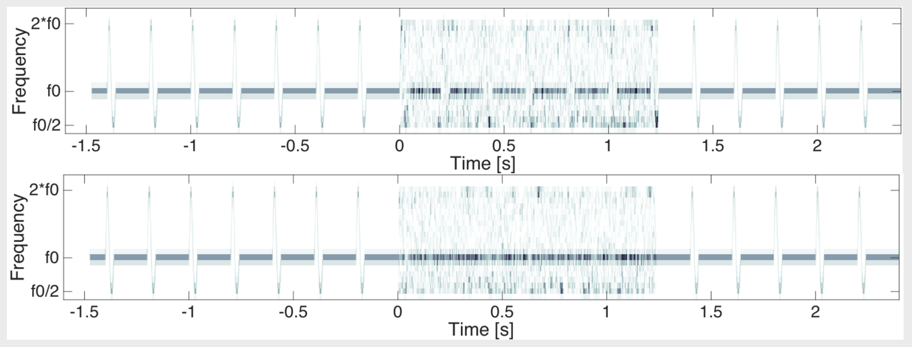


Using magnetoencephalography (MEG) we observe neural oscillations time-locked to the missing acoustic rhythms, thus reflecting entirely endogenous neural processes.

Methods

Sound stimulus. 1 hour of 5 Hz frequency-modulated (FM) narrowband carrier, 0.5 – 2 kHz range, 20% duty-cycle [2].

420 rhythmic probes (**R**) created by adding noise epochs (duration 1.24 s) to the main rhythmic sequence.



420 non-rhythmic probes (**NR**) created in the same way as (**R**), but with FM removed.

Noise spectrally-matched to FM, with SNR between -4 and 4 dB.

Detection task. Following a brief training session, $N = 35$ subjects (10 female) with no known neurological disorder or metallic implants were asked to detect target 5 Hz rhythm for every probe.

Report by button-press, post probe offset.

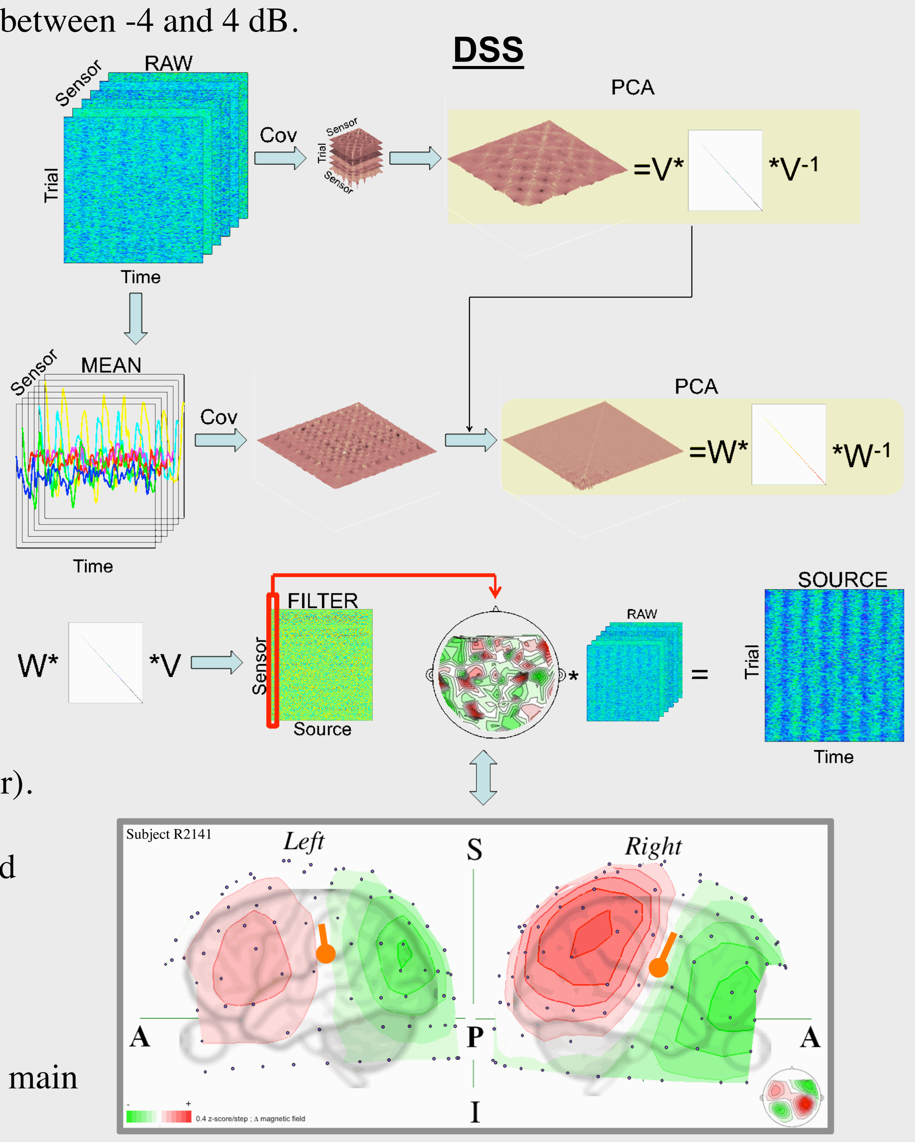
Silent film presented simultaneously.

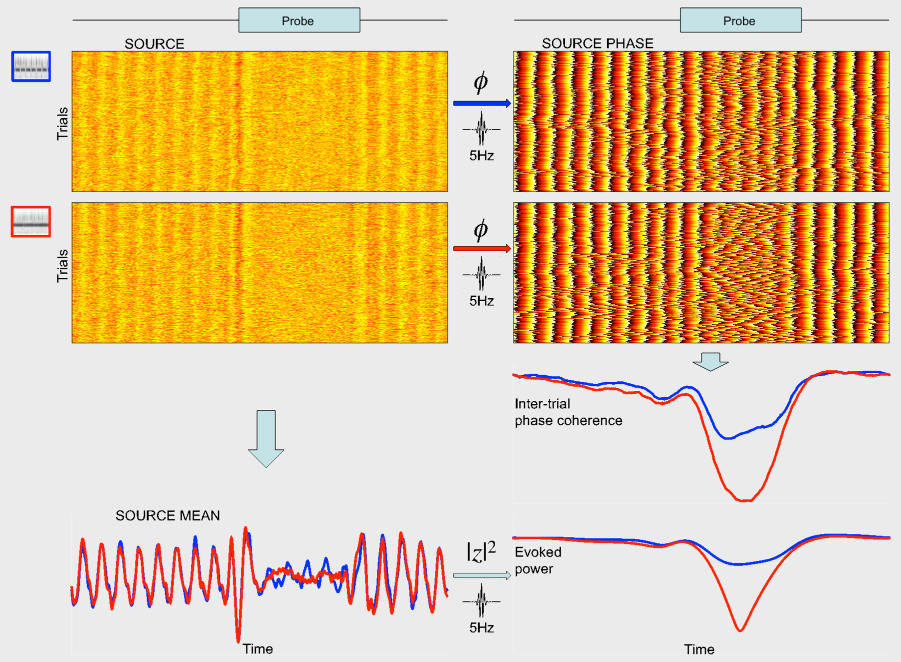
Noise probe SNR matched to participant such that detection was moderately difficult.

Signal processing. Recordings from a 157-channel whole-head KIT-MEG system (1 KHz sampling rate, 30 Hz low-pass filter).

Environment and sensor noise estimated and removed.

Data-driven spatial filters from a source separation model (DSS) [3] estimated per participant (diagram right), using data from main sound sequence (probes excluded).





Spatial filter reflecting most reproducible component of subject aSSR selected as basis for single virtual sensor.

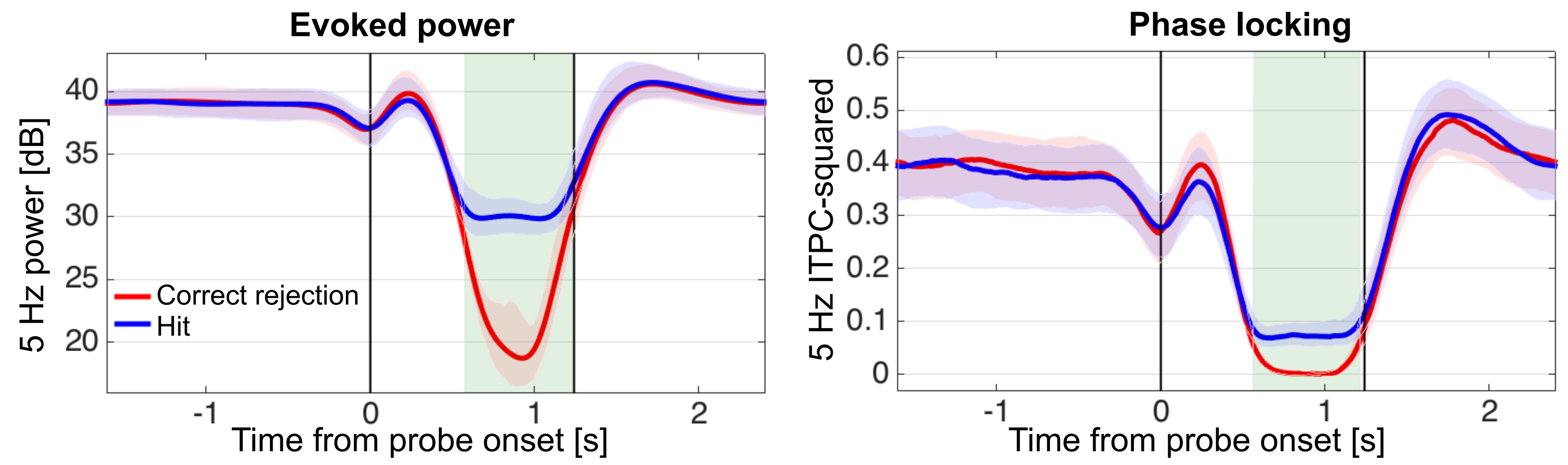
Time-frequency analysis of single trial data with Morlet wavelet corresponding to 5 Hz.

Estimation of evoked 5 Hz power and sample-size-bias corrected inter-trial phase coherence.

Statistical p-value results obtained through non-parametric permutation tests [4].

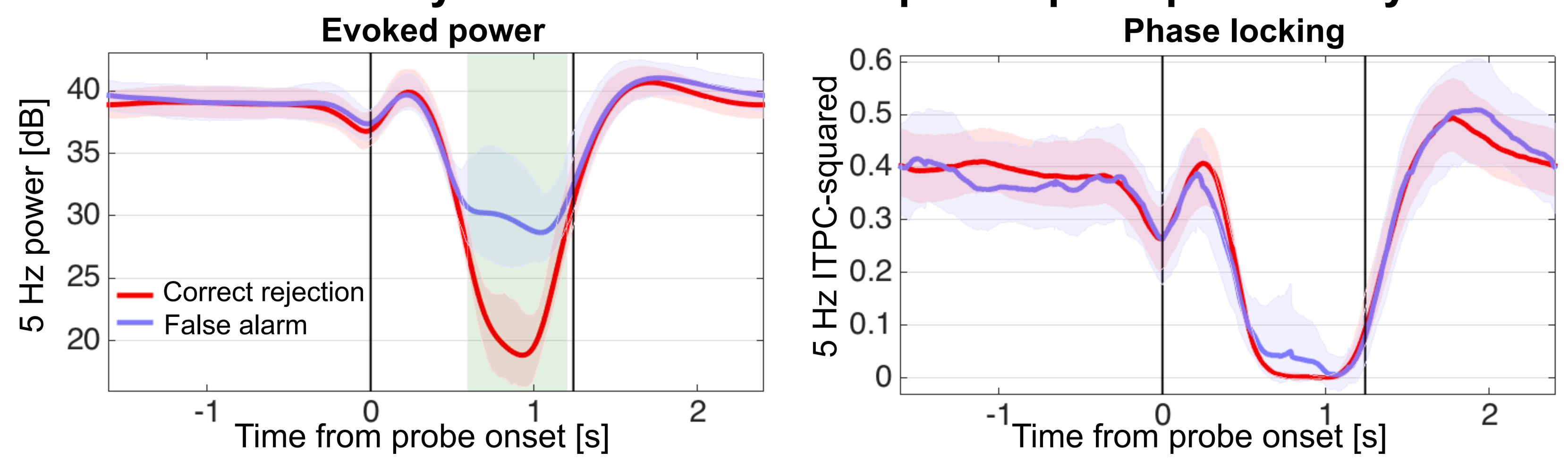
Results

1 Detection of acoustic rhythm in noise and sustained neural rhythm associated with aSSR



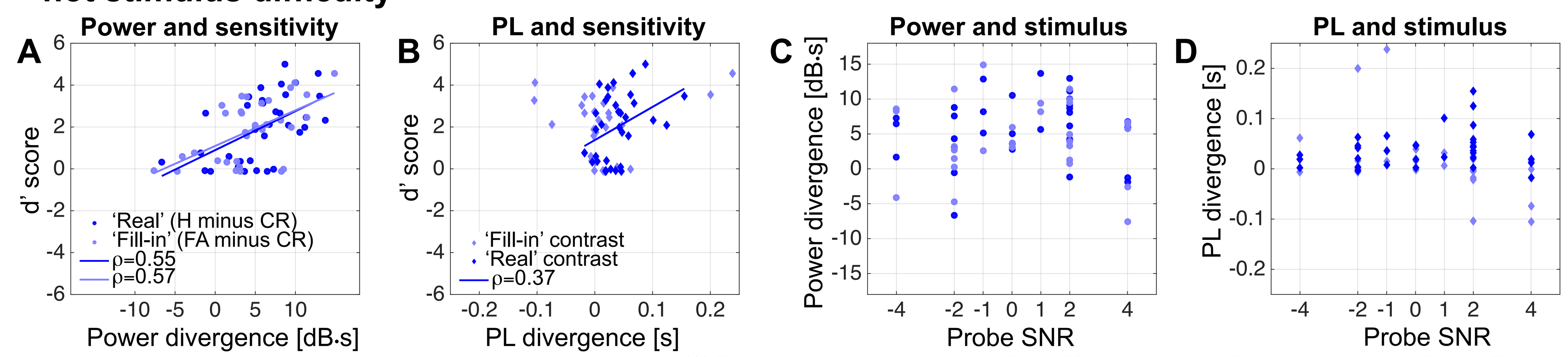
Neural responses to probes with 5 Hz rhythm (blue curves) are stronger at 5 Hz than responses to probes missing the rhythm (red curves), in both evoked power (left) and phase locking/ inter-trial phase coherence (ITPC) (right), averaged across all 35 subjects, beginning ~0.56 s post probe onset (green intervals, $p<0.001$). Black lines indicate probe edges. Correctly identified trials only. 95% confidence interval via bootstrap.

2 Power of sustained neural rhythm also relates to reported perception of rhythm



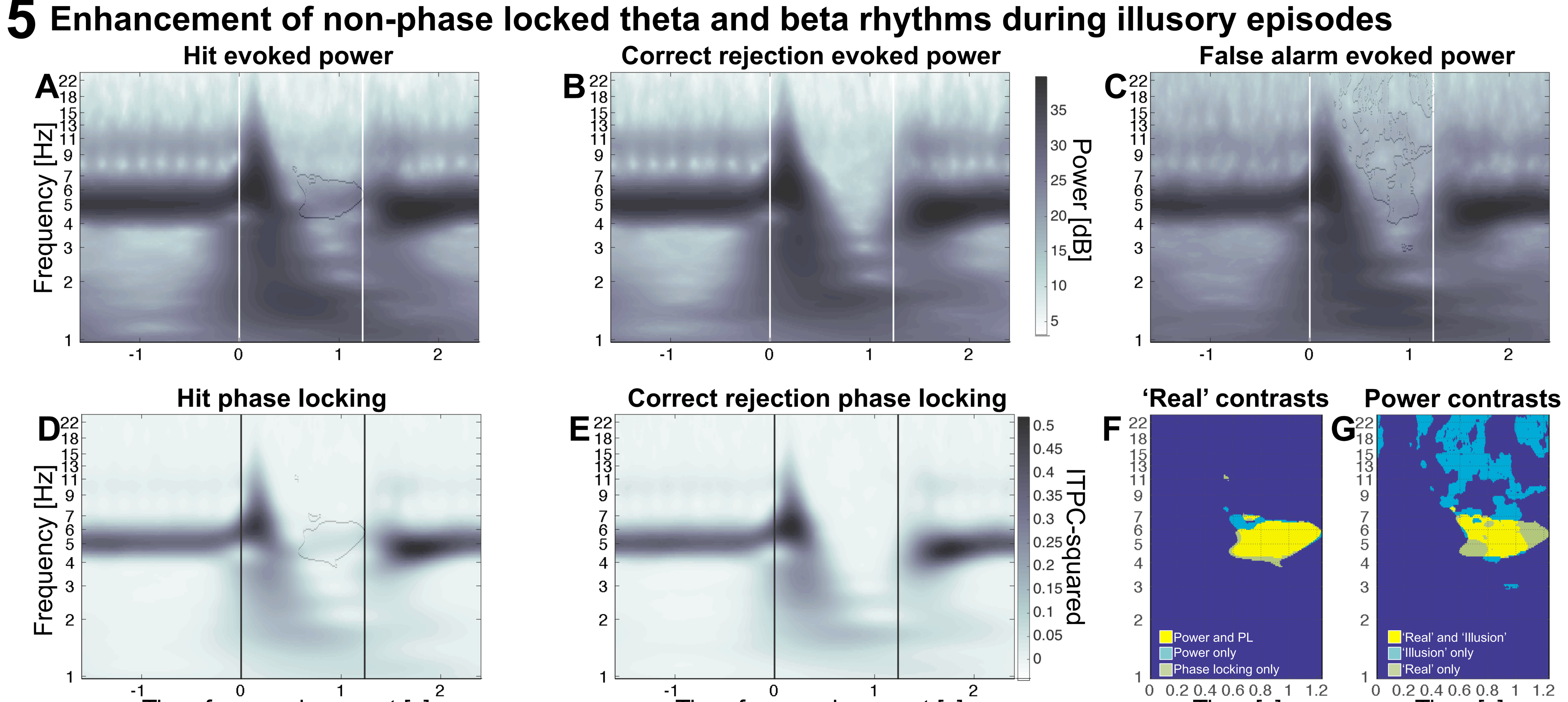
Neural responses to probes lacking the 5 Hz rhythm are stronger at 5 Hz if reported as containing the rhythm (lt-blue curves), versus correct identification (red curves), in evoked power (left) but not phase locking/inter-trial phase coherence (ITPC) (right), beginning ~0.6 s post probe onset (green interval, $p<0.001$). Averaged across 32 subjects with ≥ 5 false alarm trials. Non-rhythmic (NR) probes only. 95% confidence interval via bootstrap.

4 Percept-specific divergent processing contributes to predictability of detection performance not stimulus difficulty



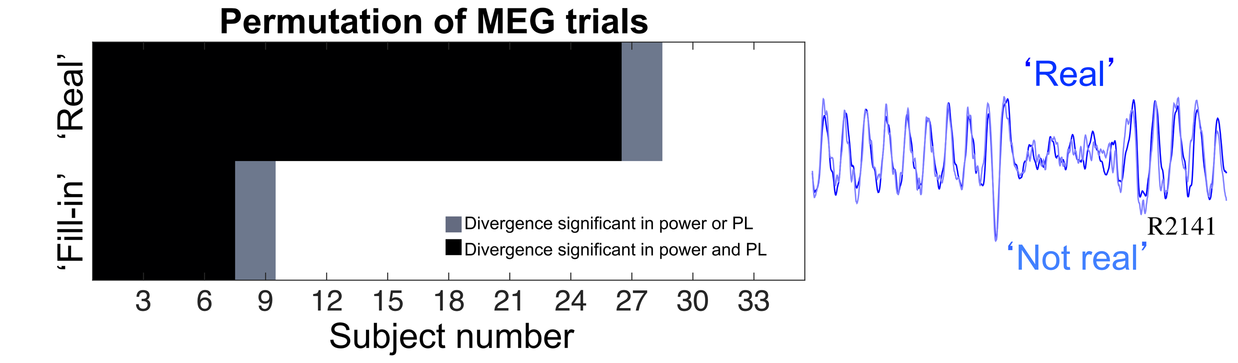
Subject-wise divergences correlate with task sensitivity not stimulus condition. **(A)** Evoked power divergences in the 'Real' (Hits minus Correct Rejections, blue) and 'Fill-in' (False Alarms minus C.R., lt blue) contrasts both correlate with task sensitivity subject-wise as measured by d' ($p<0.001$); linear regression accounts for al least 30% and 32% of variance in each contrast respectively. **(B)** Phase-locking divergences in the 'Real' (blue), but not 'Fill-in' (lt blue), contrast correlates with task sensitivity ($p<0.05$); linear regression accounts for at least 13% of variance in this contrast. None of the power **(C)** or phase-locking **(D)** contrasts were found to correlate with stimulus signal-to-noise ratio.

5 Enhancement of non-phase locked theta and beta rhythms during illusory episodes



Theta (~5 Hz) rhythms enhanced during rhythmic perception, real or illusory; beta (10-20 Hz) enhanced during illusory rhythm only. *Top row*: Power spectrograms before, during, and after **(A)** Hit, **(B)** Correct Rejection, and **(C)** False Alarm probes. Edge displays in (A) and (C) indicate spectrotemporal regions where 'Real' and 'Illusion' contrasts are significant ($p<0.05$). *Bottom row*: Phase-locking spectrograms before, during, and after **(D)** Hit probes, **(E)** Correct Rejections. Edge display in (D) indicates regions where 'Real' contrast is significant ($p<0.05$). Vertical lines indicate probe edges. **(F)** Significant regions as in (A) and (D) largely overlap in both 'Real' contrasts (power and PL) surroundingtarget 5 Hz frequency. **(F)** A significant power region as in (A) and (C) overlaps in both 'Real' and 'Fill-in' contrasts, surrounding target 5 Hz frequency; higher frequency rhythms are also enhanced for the latter contrast. All data is across subjects (N=35 or 32).

3 Observable effects of neural processing during rhythmic perception at single subject level



Trials per subject as statistical unit. *Left*: Significant ($p<0.05$) subject-wise divergences (curve area differences as in sections **1**,**2**) in the 'Real' (Hits minus Correct Rejections) and 'Fill-in' (False Alarms minus CR) contrasts, in either 5 Hz power or ITPC (black and grey), or in both (black only). *Right*: A single subject 5 Hz aSSR before, during, and after Hit (blue) and False Alarm (lt-blue) probes suggests direct synchronization to perceived rhythm during illusory trials (cf. figure in **Methods**, bottom left).

Conclusions

An auditory source tracking a low-rate sound modulation remains more active and synchronized to a target rhythm when it is perceived.

Cortical responses from that source may oscillate at rate of absent but contextually plausible rhythmic stimuli, in cases where the absent rhythm is nonetheless perceived.

This sustained, differential processing forms the basis for a potential decision variable, even observable at the single subject level. It may contribute to prediction of perceptual or behavioral outcome.

Sound modulation rate studied (slow-theta range) corresponds to syllabic timescale of human speech – raising the question of the case for synchronization to imagined/inner speech and auditory hallucinations.

Findings are at odds with proposals of auditory restoration based on suppression of slow-theta synchronization during illusory rhythms, as a mechanism for stable hearing in noisy environments [5].

Findings support the notion of dynamic interpolation from contextual information present in stimulus or present in ongoing neural rhythms; this may create an internal template that guides hearing in noisy environments.

Acknowledgments

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References

[1]Picton TW (2010) ***Human Auditory Evoked Potentials***. San Diego: Plural Publishing, Inc.
[2]Millman RE, et al. (2010) *NeuroImage*, 49(1):745–758.
[3]de Cheveigné A & Simon JZ (2008) *Journal of Neuroscience Methods*, 171(1):331–339.
[4]Maris E & Oostenveld R (2007) *Journal of Neuroscience Methods*, 164(1):177–190.
[5]Riecke L, et al. (2009) *Neuron*, 64(4): 550–561.

Poster website: http://www.ece.umd.edu/~fcc/res/illassr.pdf