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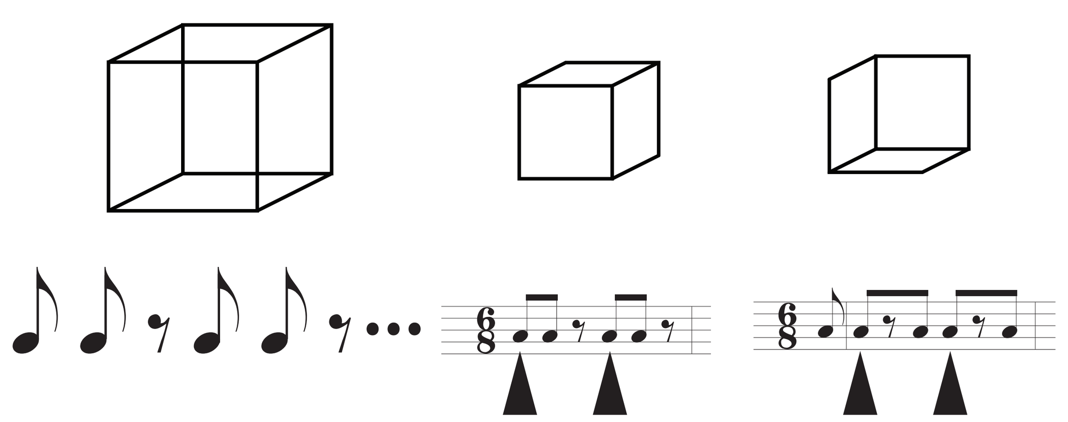
Rhythm and the Brain
Analysis of Neural Dynamics Accompanying Musical Beat Perception

J.R. Iversen[1], A.D. Patel[2], S. Makeig[1]
[1]Swartz Center for Computational Neuroscience, UCSD, La Jolla, CA; [2]Tufts University, Medford, MA.
jiversen@ucsd.edu

Introduction

We actively shape our perception of the world.

Beat-based processing: The perception of musical rhythm, in particular, is strongly shaped by our active interpretation: where we feel the pulse or "the beat."



Rhythm: Temporal pattern of events

Beat: Internally generated interpretation
- Timing of beat can be modified at will (phase shift)
  - Radically changes perceptual experience
- Confers major cognitive advantages
- Organizes movement

The beat is often implied by physical accents in music, but in the absence of physical cues the location of the beat can be ambiguous. In such cases, a listener can willfully impose a beat, and thus organize and dramatically alter the perceptual rhythm. How does the brain selectively interpret some events as beats?

A background question is whether the mechanisms for self-imposing an imagined beat are purely auditory, or may involve the motor system in the generation of 'covert action' (Repp, 2006; Repp & Penel, 2004). In support of this idea, evidence has shown activity in motor planning regions when listening, but not moving to, a rhythm that evokes a strong sense of beat (e.g. Grahn & Rowe, 2009). Still, the milisecond dynamics of any such interactions between auditory and motor systems, and how it might exert effects on perception, is unknown.

How is the conscious interpretation of a rhythm reflected in brain activity?

Experimental Design

Beat creation in syncopated rhythms
What marks a beat in absence of stimulus?

Specific question:

What regions of the brain preferentially respond to the internally generated beat vs the external sound?

We designed a task to *decouple* the timing of external stimuli and the sought-after internal process of the beat.

We addressed this question by measuring stimulus-evoked brain responses as listeners manipulated their metrical interpretation of an unchanging simple rhythmic stimulus (Iversen, et al., 2009). As the stimulus was invariant, differences in brain activity relate to metrical interpretation.

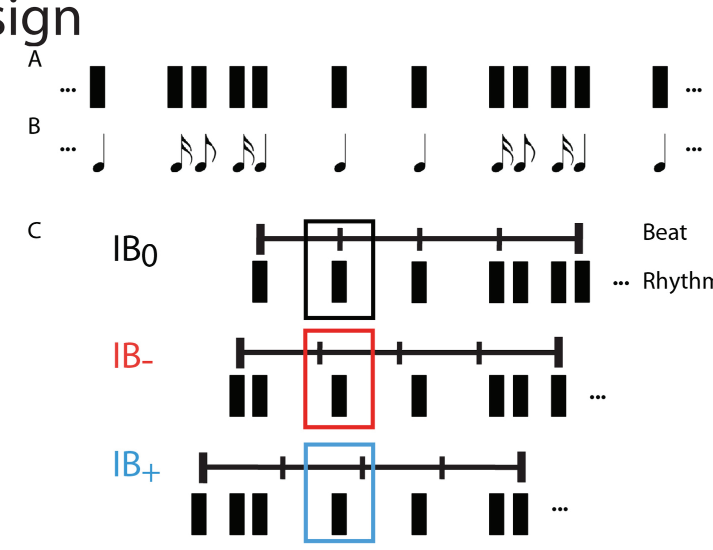
The present design also elminates the confound present in past work that the beat always occurs along with a sound. Here, we shift the location of the beat with respect to the stimulus.

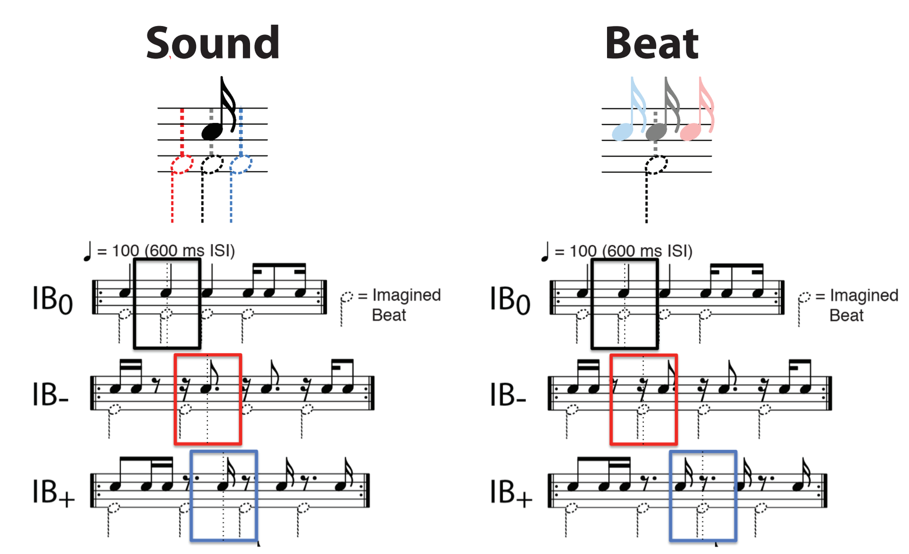
Methods

Task and Stimulus

Musically trained listeners (n=14) internally placed the beat in one of three phases within an unchanging rhythm. Two beat positions yielded a highly syncopated rhythm in which the beat was not marked by a tone. Compliance with the task was verified by tapping the beat occasionally throughout the trial.

Design





Behavioral verification: Listeners were instructed not to move or use motor imagery. Listeners were instructed to tap the beat occasionally throughout a trial (about once per minute, tapping four beats). The asynchrony of taps relative to the correct beat were calculated and any trials with asynchrony > 75 ms were excluded. Four of 14 participants were unable to hold the syncopated beat, and were excluded from

Stimulus details: Rhythmic pattern made of identical tones; shortest IOI was 150 ms, and beats occurred every 600 ms. The beat was initially indicated by a 500 Hz tone that played along with the rhthm for 12 beats to cue the condition. The Rhythmic pattern was shifted with respect ot the induction beat, yielding a different relationship between beat and rhythm for each condition. The perception of the three resulting rhythms was different, and listeners were generally not even aware that it was the same undrelying rhythm

Analysis of brain responses

Brain activity was measured continuously using magneto-encephalography (MEG, 148 channels).

Independent source components (ICs) were seperated using ICA (Makeig, et al. 1997), after first rejecting data segments containing sensor flux jumps.

Sound-evoked IC responses were computed by averaging epochs aligned to the first tone of the repeated phrase.

Beat-evoked responses were inferred by realigning epochs to the presumed beat location.

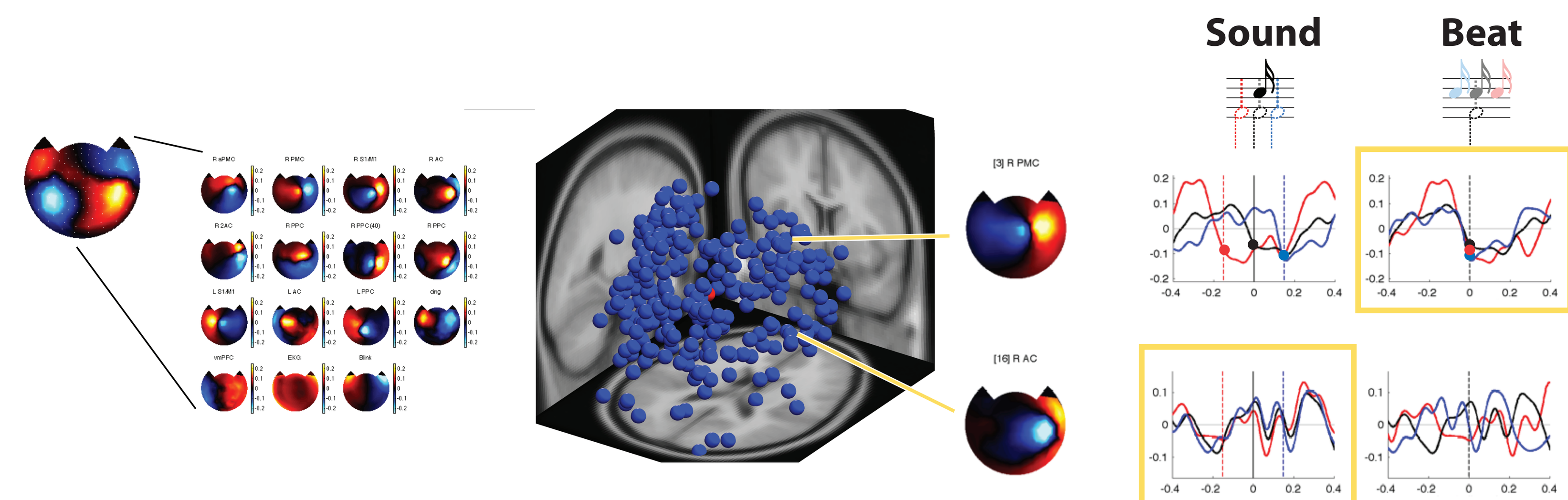
Classification of response character using ratio of pairwise rms differences, cluster analysis, and measure projection on ERPs

To enable localization of activity, head shape and location were digitized. Sources were localized using equivalent dipole fitting using normalized, reduced-rank leadfields generated from a template head model warped to the digitized head shape (Akalin Acar and Makeig 2010). Multiple runs were combined after spatial realignment and projection to a standard sensor array. (Fieldtrip toolbox for EEG/MEG-analysis, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, the Netherlands. See http://www.ru.nl/neuroimaging/fieldtrip).

Cross-subject source level analyses were constructed by warping dipole locations to a common template space, and applying principal component analysis clustering (Makeig, et al., 2004), or measure projection (Bigdely-Shamlo et al. 2013) to define differential functional domains.

Results

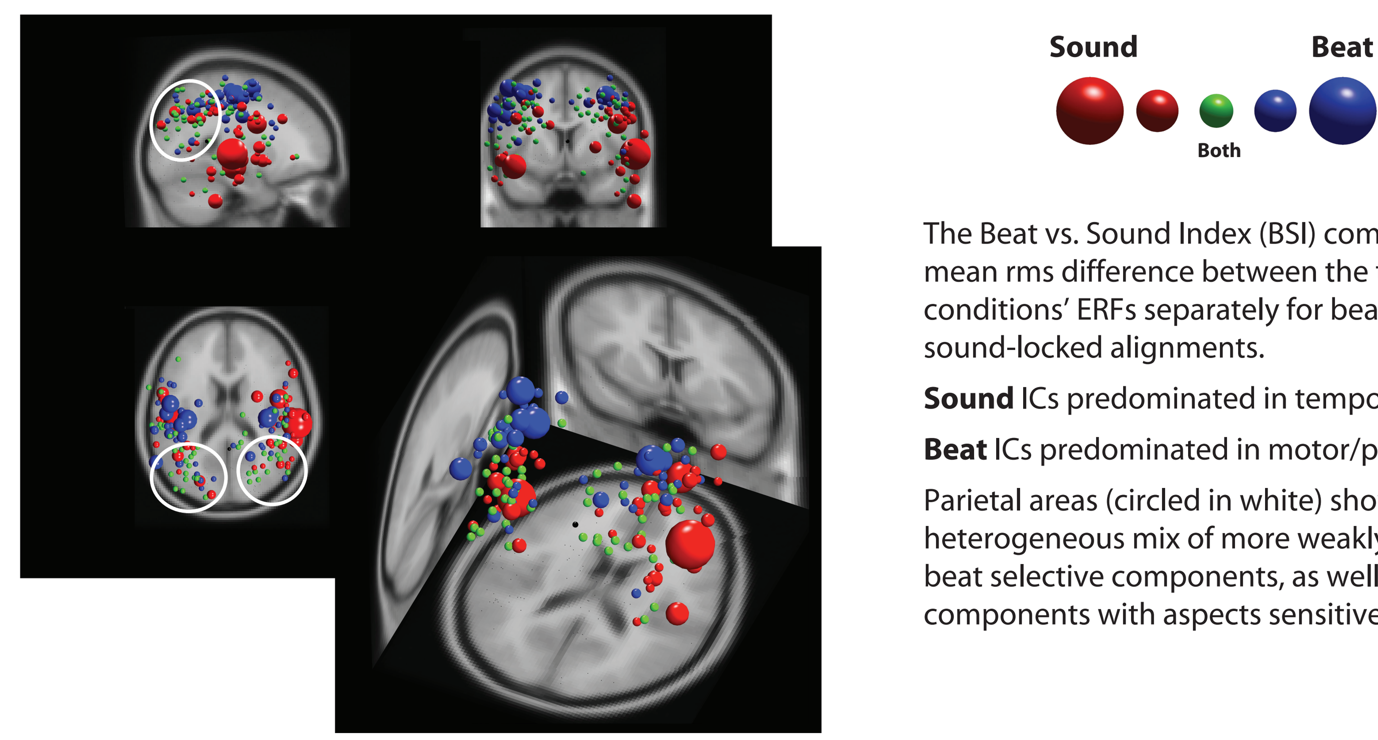
Source Distribution



ICA yielded an average of 28 (range 16 to 41) strongly dipolar components (rv < 0.15) localized within the brain volume. ICA also readily seperated blink, channel and cardiac artifacts.

Individual IC examples of strongly beat-locked and strongly sound-locked ERFs.

Classification of sound and beat regions



The Beat vs. Sound Index (BSI) compares the mean rms difference between the three conditions' ERFs separately for beat- and sound-locked alignments.

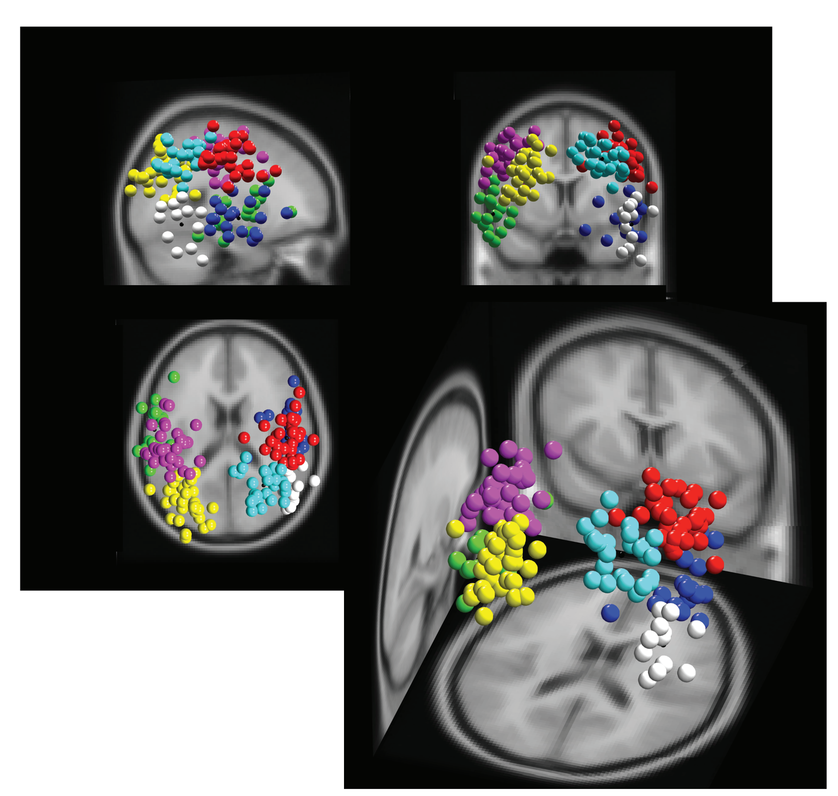
Sound ICs predominated in temporal cortex

Beat ICs predominated in motor/premotor cortex.

Parietal areas (circled in white) show a more heterogeneous mix of more weakly sound and beat selective components, as well as a class of components with aspects sensitive to both.

The BSI is the log ratio of mean beat and sound rms differences. Large positive values (red) indicate that the ERFs line up more when aligned to the sound onset; negative values (blue) indicate ERFs that line up more when aligned to the imagined beat. Green indicate components with low rms mismatch for both sound and beat alignments, meaning they have ERF features that are timelocked both to sound and beat. (15% / 11% of ICs were strongly sound / beat responsive (|z|>1)).

Component clustering

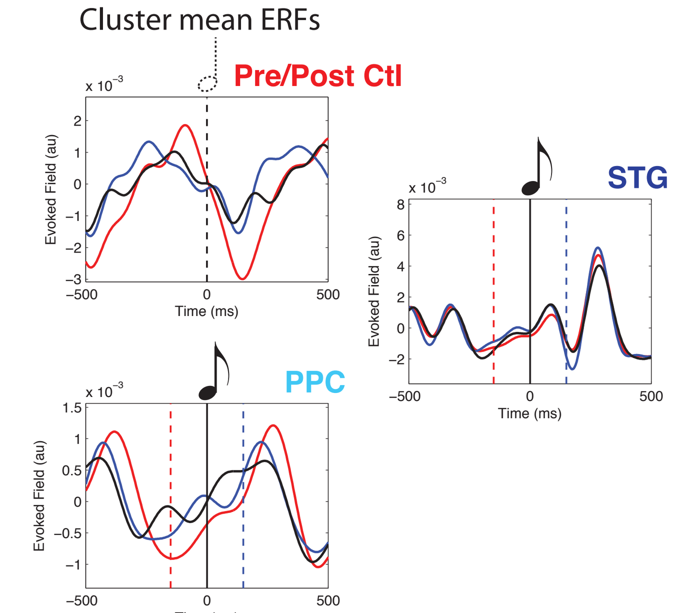


K-means clustering with k = 12. IC features were a weighted sum of dipole position and PCA reductions of ERP, ERSP, ITC, and spectrum. Dipole position was weighted 10x, and ERP 2x vs. the other features. Five clusters are not shown: three occipital alpha clusters, and eye-related cluster, and a diffuse, deep cluster.

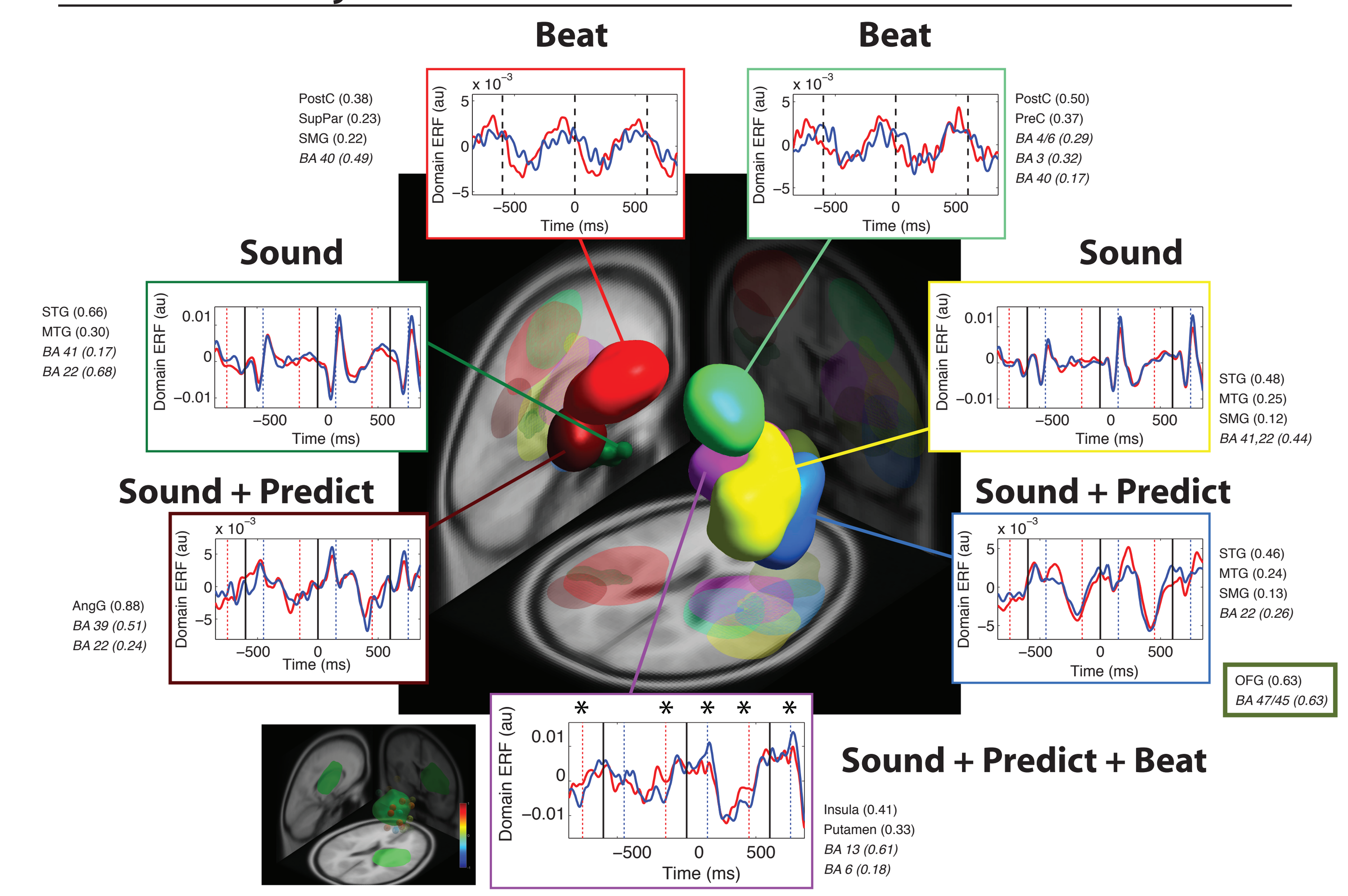
Components were k-means clustered using a feature vector composed of a reduced-dimensionality composite of location, ERP, ERSP and spectra.

Clustering yielded anatomically plausible clusters bilaterally in somatomotor/ premotor cortex, temporal cortex, and parietal cortex

Cluster mean ERFs



Measure Projection



Measure Projection (Bigdely-Shamlo, et al, 2013) is a newly described statistical method that finds volumetric domains with high, consistent similarity of a component measure, in this case the ERF. Here, domains and their exemplar ERF are shown (MP parameters: p<0.075, max correlation 0.6). *=significant difference between IB- and IB+ (p<0.05). MP is not sensitive to regions with heterogenious responses, e.g. posterior parietal seen in the classification analysis.

Discussion

ICA decomposed responses to beat perception task into consistent, functionally distinct classes of localized responses

Beat related: activity that preceded the internal beat event

Sound related: activity evoked by sound

Beat-related activity prominent in somatomotor & parietal cortex

Consistent with motor role in beat perception.

Outstanding questions

Imagined or unintended movement?

Causal influence on auditory processing?

Higher-order predictive and integrative activity in parietal and medial temporal cortex.

Parietal as a potential locus of auditory-motor interaction is supported by physiological (Pollok, 2005; Fujioka, et al, 2012) and anatomical findings (Gierhan, 2013).

The right medial MP domain showed features responsive to both sound and beat. This domain overlaps most with Insula, striatum, and premotor cortices.

References

Akalin Acar Z, Makeig SD (2010) Neuroelectromagnetic forward head modeling toolbox. J Neurosci Methods 190:258–270.

Bigdely-Shamlo N, Mullen T, Kreutz-Delgado K, Makeig SD (2013c) Measure projection analysis: a probabilistic approach to EEG source comparison and multi-subject inference. NeuroImage 72:287–303.

Delorme A, Mullen T, Kothe CA, Akalin Acar Z, Bigdely-Shamlo N, Vankov A, Makeig SD (2011) EEGLAB, SIFT, NFT, BCILAB, and ERICA: New Tools for Advanced EEG Processing. Comput Intell Neurosci 2011:1–12.

Gierhan SME (2013) Connections for auditory language in the human brain. Brain Lang. 10.1016/j.bandl.2012.11.002.

Grahn JA, Brett M (2007) Rhythm and beat perception in motor areas of the brain. J Cogn Neurosci 19:893–906.

Iversen JR, Repp BH, Patel AD (2009) Top-down control of rhythm perception modulates early auditory responses. Ann N Y Acad Sci 1169:58–73.

Large, E.W., and Jones, M. R. (1999). The dynamics of attending: How we track time varying events. Psychological Review, 106, 119–159.

Makeig S., Jung T.P., Bell A.J., Ghahremani D., Sejnowski T.J. (1997) Blind separation of auditory event-related brain responses into independent components. Proc Natl Acad Sci U S A 94:10979-10984.

Makeig SD, Debener S, Onton J, Delorme A (2004) Mining event-related brain dynamics. Trends Cogn Sci 8:204–210.

Mayville, J.M., Fuchs, A., Ding, M., Cheyne, D., Deecke, L., and Kelso, J.A.S. (2001). Event-related changes in neuromagnetic activity associated with syncopation and synchronization timing tasks. Human Brain Mapping, 14:65-80.

Pollok et al. (2005) The oscillatory network of simple repetitive bimanual movements. Brain res Cog brain res 25:300-11

Repp, B.H. (2007). Multistability of metrical interpretation, reflected in rate limits of sensorimotor synchronization. Cognition 102: 434-454.

Acknowledgements

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