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Entrainment of Premotor Cortex Activity by Ambiguity in Musical Metre

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Background

Musical rhythm tends to be organized in a metric structure, usually consisting of periodic salient positions (beats). Metric beats are anticipated by neural processing, as demonstrated by previous research showing that metric beats coincide with increased attention (Jones, et al., 2002) and impact of movements (e.g. foot-tapping).

Motor areas of the brain, including basal ganglia, premotor area, and supplementary motor area, have been implicated in the perception of musical rhythms (e.g. Grahn and Brett, 2007). Previous electroencephalographic (EEG) research has shown modulation of gamma band (24-60 Hz) activity with the metric beat during listening to rhythmic tone sequences (Snyder and Large, 2005; Fujioka, et al., 2009). These findings reflect anticipatory brain activity in response to auditory rhythms. Other research has shown that for isochronous auditory sequences, amplitude is increased for frequencies that match the endogenously generated metric beat (Nozaradan, et al., 2011), and inter-trial phase coherence (ITC) is increased at the frequency of the stimulus sequence (Will and Berg, 2007). One limitation of previous EEG studies on rhythm and metre processing is the use of isochronous tones as stimuli, which does not capture the full extent of metre processing of non-isochronous sequences, as in musical rhythm.

Aims

This study aims to investigate how neural processing of rhythm, as measured by amplitude and ITC of EEG, varies as a function of the metrical ambiguity of the stimulus.

Method

Twenty musicians underwent 32 channel EEG recording as they listened to two versions of Steve Reich's *Clapping Music,* a piece of rhythmic music consisting of two performers clapping 12 distinct rhythms, each repeated 12 times. The rhythms in this music are either metrically ambiguous (fitting equally well to metres of 3 or 4 beats) or unambiguous (fitting best to a metre of 3 beats), according to a model of metre induction (Povel and Essens, 1985).

Using a fast Fourier transform, amplitude and ITC values were extracted from EEG, aligned with each repetition of each rhythmic figure. Amplitude and ITC values were analyzed for main effects and interactions of *stimulus version*, *frequency band* (delta, theta, alpha, beta, and gamma), *metric ambiguity*, and *scalp distribution* (4 quadrants), using repeated measures analyses of variance (ANOVA). Source analysis was used to investigate the likely neural sources of effects of interest, using the BESA® software package.

Further analyses investigated differences at narrow frequency bands centred on the specific frequencies of the 2 possible metric beats of the stimulus (1.33 Hz and 1.77 Hz).

For all analyses, ANOVA were Huynh-Feldt corrected and follow up contrasts used Tukey corrected paired t tests.

Results

Results showed significant 3 way interactions of scalp quadrant, frequency band, and metric ambiguity for both amplitude (F (4,76) = 2.46, p < .05), and ITC (F (4,76) = 14.10, p < .001). Follow up contrasts (Tukey corrected) show that ambiguous rhythms generate significantly greater amplitude compared to unambiguous rhythms, in frontal electrodes in the delta band (1-4 Hz) (t (19) = 3.13, p < .05). ITC is also greater for ambiguous rhythms in frontal electrodes in the delta band (t (19) = 4.92, p < .001). In the alpha band (8-12 Hz), ambiguous rhythms elicit lower amplitude responses than unambiguous rhythms (t (19) = -3.47, p < .05). Based on examination of topographical plots of the scalp distribution of effects, we also performed a paired t test on gamma band amplitude over electrodes located most laterally on both sides, on the central line. Gamma amplitude is greater in these electrodes for ambiguous compared to unambiguous rhythms (t(19) = 2.49, p < .05).

Results of ANOVA for metre-specific frequencies (1.33 Hz and 1.77 Hz) shows significant interactions of scalp quadrant and ambiguity (F(3,57) = 8.98, p < .001), and of scalp quadrant and frequency (F(3,57) = 4.15, p < .05) for ITC, and significant interaction of scalp quadrant and ambiguity (F (3,57) = 4.00, p < .05). Follow up contrasts show that ITC is significantly greater in frontal electrodes for ambiguous rhythms at 1.33 Hz (t(19) = 3.83, p < .01) and at 1.77 Hz (t(19) = 3.29, p < .01). Amplitude is also greater in frontal electrodes for ambiguous rhythms at 1.33 Hz (t(19) = 1.76, p = .09) and at 1.77 Hz (t(19) = 2.99, p < .01).*

Topographical plots of ambiguity-based differences (ambiguous - unambiguous) in delta amplitude, delta ITC, alpha amplitude, and gamma amplitude are shown in Fig 1.

Results of the source analysis for differences in ITC in the 1.25-1.75 Hz band indicate that dipoles may be located in right inferior frontal gyrus (x=57, y=10, z=22) and left ventral premotor cortex (x=-62, y=4, z=27). Images showing the location of sources associated with this difference are found in Fig 2.

*Though results for amplitude of one frequency (1.33 Hz) is marginally above the nominal threshold of statistical significance, we take this as reflecting a meaningful difference, since it is consistent with other effects.

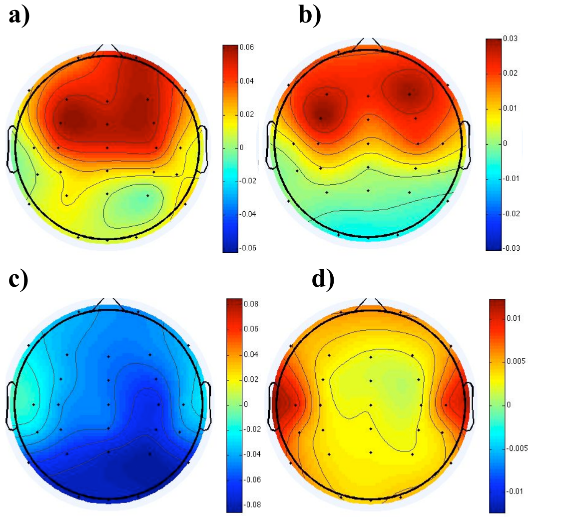

Figure 1. Topographical scalp distributions for differences between metrically ambiguous and unambiguous rhythms in a) delta amplitude, b) delta ITC, c) alpha amplitude, and d) gamma amplitude.

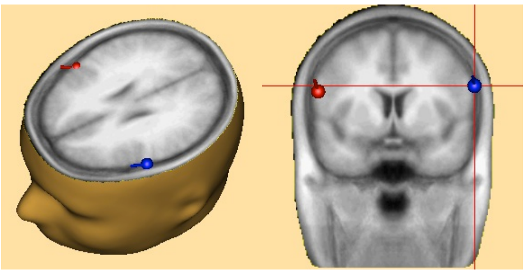

Figure 2: Images constructed source analysis, showing the most likely dipole locations for ambiguity-based differences in ITC in the 1.25-1.75 Hz band. These locations are right inferior frontal gyrus (BA45) and left ventral premotor cortex (BA6).

Conclusions

Our results show characteristic changes in EEG responses during musical listening, corresponding to differences in the metric information present in musical rhythms. We find effects in amplitude and ITC at the frequency of the metric beat of rhythmic sequences (1.33 Hz and 1.77 Hz), consistent with previous research (Nozaradan, et al., 2011; Will and Berg, 2007; for amplitude and ITC, respectively) and modulation of gamma amplitude with metric differences in rhythms, also in agreement with previous research (Snyder and Large, 2005; Fujioka, et al., 2009). Furthermore, the apparent brain and scalp distributions of these effects are consistent with previous research showing effects of metrical structure in gamma amplitude response generated in primary auditory cortex (Fujioka, et al., 2009). Changes in amplitude and ITC of metre-specific frequencies appear to be generated bilaterally in ventral premotor area and inferior frontal gyri. This is consistent with previous research showing the ventral premotor area as a site of activity during the aesthetic appreciation of musical rhythmic sequences (Kornysheva, et al., 2010). This area has also been linked to domain-general anticipatory processing for hierarchical sequences (Fiebach and Schubotz, 2006). Our findings are consistent with this, since we show effects related to the metric structure of rhythmic sequences (hierarchical organization of anticipated salient time points in a temporal sequence).

These results represent a significant advance over previous research because the stimuli used were real-world non-isochronous musical rhythms, rather than artificial isochronous sequences, as well as showing changes in both amplitude and ITC of metre-specific frequencies in motor areas of the brain.

Amplitude in the alpha band showed the opposite pattern to other frequency bands, in that it was lower for metrically ambiguous rhythms than unambiguous. This may reflect anticipatory processing due to greater metric information of rhythmic sequences, since reduction of alpha power has been observed during temporal anticipation (Rohenkohl and Nobre, 2011).

Future research should investigate similar effects of metre on EEG using perceptual and behavioural methods (i.e. a synchronized tapping task) to correlate individuals' explicit metre-perception with amplitude and ITC of EEG at particular frequency bands. Moreover, rhythmic figures should be presented in random order rather than the same order for both versions and all participants. This will eliminate any possible order effects of rhythms on EEG. It is also important to investigate how neural responses vary to systematically manipulated metrical strength, since metric rhythms differ not only in *which* metre fits, but how strongly a metric beat is induced.

Keywords

Metre processing; Rhythm; Entrainment;

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