Beta and Gamma Rhythms in Human Auditory Cortex during Musical Beat Processing

Takako Fujioka,[a,b] Laurel J. Trainor,[a,b] Edward W. Large,[c] and Bernhard Ross[a]

[a]*Rotman Research Institute, Baycrest, University of Toronto, Toronto, Ontario, Canada*

[b]*Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, Ontario, Canada*

[c]*Center for Complex System and Brain Sciences, Department of Psychology, Florida Atlantic University, Boca Raton, Florida, USA*

We examined β- (~20 Hz) and γ- (~40 Hz) band activity in auditory cortices by means of magnetoencephalography (MEG) during passive listening to a regular musical beat with occasional omission of single tones. The β activity decreased after each tone, followed by an increase, thus forming a periodic modulation synchronized with the stimulus. The β decrease was absent after omissions. In contrast, γ-band activity showed a peak after tone and omission, suggesting underlying endogenous anticipatory processes. We propose that auditory β and γ oscillations have different roles in musical beat encoding and auditory–motor interaction.

Key words: **neural oscillation; magnetoencephalography; event-related desynchronization (ERD); musical beat; auditory–motor interaction**

Introduction

From complex rhythmic patterns, listeners can establish a mental representation of a steady beat and put it into a metric interpretation of strong and weak accents (e.g., perceiving 2-beat or 3-beat groups). Auditory discrimination is more accurate on an accented beat and more readily processed than on unaccented beats, suggesting that strong beats attract attention.[1] The accuracy of synchronized tapping to a beat can best be maintained at intervals of 200–1800 ms, with a maximum at about 600 ms.[2,3] Thus physiological mechanisms specifically dedicated to auditory–motor interaction for rhythmic perception and production exist and constrain our behavior and involve various cortical and subcortical areas.[4] However, little is known about the encoding mechanisms that both auditory and motor systems access.

Candidates for such neural correlates include dynamic changes in rhythmic neural activities observed in electroencephalography (EEG) and magnetoencephalography (MEG). Rhythmic neural activity reflects communication between brain regions, such as neocortex and thalamus,[5] and modulates with sensory and cognitive processes.[6,7] Of particular interest are β- (15–30 Hz) and γ- (>30 Hz) band activities. Modulation of β oscillation is widely associated with motor tasks and has been observed in sensory and motor cortices[6,7] as well as in the basal ganglia, cerebellum, and motor periphery in animals and humans.[8]

The γ oscillation around 40 Hz is the most favored rhythm in the auditory cortex[9] and is enhanced for meaningful stimuli (i.e., phonemes) compared to pure tones during

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Address for correspondence: Takako Fujioka, Ph.D., 3560 Bathurst Street, Toronto, Ontario, M6A 2E1, Canada. Voice: +1-416-785-2500x3413; fax: +1-416-785-2862. tfujioka@rotman-baycrest.on.ca

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discrimination.[10] Induced γ-band activity, which is not strictly phase-locked to the event, has been related to object-feature binding in visual tasks,[11] suggesting a connection to endogenous processes.

Auditory cortex β-band activity has not been observed during passive listening. A previous EEG study found periodic modulation of 20–60 Hz activity synchronized to a pulse with a duple metric accent.[12] Some individuals showed increased activity even before the tone onset or after its omission. However, its generator loci and separation between β and γ oscillation remain unclear. The present study separately examined β- and γ-band activity in auditory cortices recorded by MEG using the stimuli of Snyder and Large.[12] We assessed the effect of accent and omission of accented and unaccented beats. We hypothesized that β-band modulation may be observed in auditory cortices, and that β- and γ-band modulations may be differently associated with tones and omissions.

Methods

Twelve healthy young adults without extensive musical experience participated in the study. Stimuli were 262-Hz pure tones, 60 ms in duration, including 10-ms rise/fall time, with an interval (onset-to-onset) of 390 ms presented 60 dB above individual sensation levels binaurally. Every second tone was reduced in intensity by 6 dB to make an alternating loud–soft accent pattern. Subjects listened passively to eight 400-s blocks, in which half of the blocks occasionally (30%) omitted the loud tone, and half the soft tone (Fig. 1), while he or she watched a silent subtitled movie.

MEG was recorded with a 151-channel whole-head MEG (VSM MedTech Ltd., Port Coquitlam, BC, Canada) sampled at 1250 Hz and on-line low-pass filtered at 400 Hz. Large artifacts were removed by principal component analysis.[13] Auditory evoked magnetic fields were first averaged in the time domain and used for auditory source estimation as equivalent current dipoles in bilateral temporal lobes performed on the peak around 80 ms (P1m), the most prominent peak on account of the fast stimulation rates. For each subject the source model was used as a spatial filter[9,14] to transform all single-trial magnetic field data into time-varying source waveforms in each hemisphere.

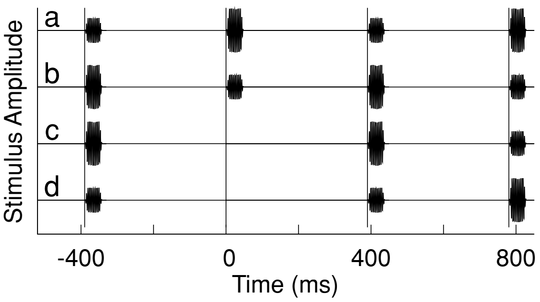

Figure 1. (**a–b**) Stimulus sequences of alternating loud and soft tones with intervals of 390 ms. (**c–d**) Omission of a soft and a loud sound, respectively.

Time–frequency decomposition using Wavelet analysis was performed on these source waveforms with a −800- to 800-ms time interval and a 6.25- to 125-Hz frequency interval. The time-domain averaged response was subtracted before the decomposition to specifically assess induced activity, although the trial-to-trial variance of the evoked component cannot be eliminated.[15]

Results

Stimulus related changes in β- and γ -band in auditory cortex were observed in all subjects and all conditions (loud, soft, loud-omission, soft-omission). Since there were no significant differences between loud and soft cases, the responses were averaged across tones and across omissions. The β power showed a periodic modulation with a decrease after each stimulus onset that reached a minimum around 200 ms and returned to baseline before the next stimulus onset (Fig. 2). However, the decrease was absent in the case of

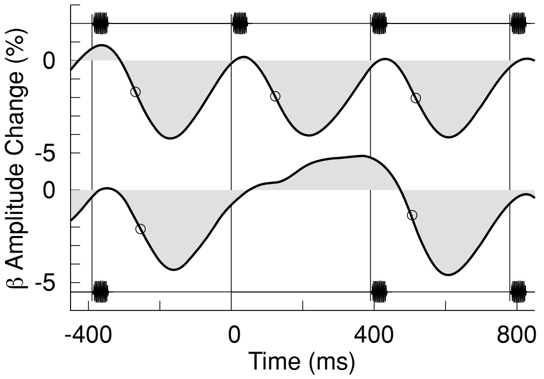

Figure 2. Event-related changes in β (15–20 Hz) activity for the stimuli (top) and the omission (bottom).

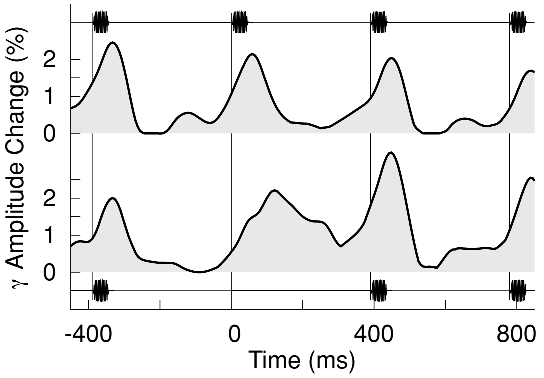

Figure 3. Event-related changes in γ (28–48 Hz) activity for the stimuli (top) and the omission (bottom).

omission. To assess this decrease, the amplitudes of β activity at 20 ms and 200 ms were submitted to a repeated-measures ANOVA with the factors "hemisphere" (left versus right), "stimulus" (regular versus omission), and "latency" (20 versus 200 ms). There was a significant main effect of latency [$F(1,11) = 6.14$, $P = 0.031$] and an interaction between latency and stimulus [$F(1,11) = 7.03$, $P = 0.023$], with significant β decrease for the regular stimuli [$t(12) = 2.8$, $P = 0.017$], but not after the omission [$t(12) < 2.0$]. No other interactions were observed.

The γ-band activity showed a distinct peak at 80 ms after each tone (Fig. 3) and also in the case of sound omission at 110 ms. The peak amplitudes of γ activity were significantly larger for both stimuli [$t(12) = 2.61$, $P = 0.023$] and omission [$t(12) = 2.75$, $P = 0.018$] when compared to the prior level of γ activity measured at the midpoint of the preceding stimuli (−185 ms).

Conclusions

The isochronous auditory stimuli induced changes in β and γ oscillation in auditory cortices. The β modulation remained synchronized with the stimulus pulse except when an omission disrupted this regular pattern, resulting in an excessive increase. In self-paced motor tasks, β oscillation decreases preceding movements by one or more seconds.[6,7] Moreover, it is easier to initiate a new movement when β is suppressed compared to when β is increased.[16] The β suppression observed occurs automatically because our subjects were not engaged in any motor tasks. We propose that β-band activity in auditory cortex may help to signal timing cues to facilitate motor preparatory processes for sound synchronization, such as in dancing. Further research should determine the pathways for such auditory–motor interaction.

The γ activity has also been hypothesized to mediate functional connectivity between brain regions. The increase of γ immediately after the tones resembles that of the typical evoked γ-band response.[17] Since the subtraction of the evoked response does not remove its variance entirely, this early γ peak could still contain the evoked component to some extent. More importantly, a γ peak occurred, although with a longer latency, when the stimulus was absent. This is in sharp contrast to the β-band behavior and suggests that the γ activity may reflect an endogenous process. One possibility is that the regular auditory pulse entrains intrinsic γ activity to its tempo and continues during a tone omission, thus representing anticipated stimulus timing.

We propose that in the auditory cortex the β rhythm may play a role in auditory–motor communication and reflect a largely exogenous process, while the γ rhythm involves endogenous processes related to musical beat encoding and anticipation of the next pulse.

However, it is highly likely that oscillatory activities are spread spatially across brain areas and are not limited to the auditory cortical sources analyzed here. Further multiple source analyses would be informative for better understanding of auditory–motor interactions in music perception.

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Conflicts of Interest

The authors declare no conflicts of interest.

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