Proceedings of the 8th International Conference on Music Perception & Cognition, Evanston, IL, 2004
ICMPC8
S.D. Lipscomb, R. Ashley, R.O. Gjerdingen, & P. Webster (Eds.)
Adelaide, Australia: Causal Productions

GAMMA-BAND ACTIVITY DURING PERTURBED TONE SEQUENCES: AN EEG STUDY

Theodore P. Zanto, Edward W. Large, Armin Fuchs, & J.A. Scott Kelso

Center for Complex Systems and Brain Sciences, Florida Atlantic University

ABSTRACT

We study the relationship between cortical gamma-band activity (GBA) and perturbations of isochronous tone sequences, using electro-encephalography (EEG). Participants listened attentively to isochronous tone sequences in which temporal perturbations occurred every 6-10 tones. At the perturbation location, tones occurred early, on-time, or late. The responses to early vs. late tones were markedly asymmetric. Early tones resulted in a greater increase in GBA power at the locus of the perturbation than on-time or late tones. The latency of GBA relative to tone onset also depended asymmetrically on the direction of the perturbation. Our observations indicate that early tones produced long latencies while late tones yield a short (and often anticipatory) peak latency. The current results provide evidence supporting the role of GBA in temporal expectancy. Thus, GBA is a good candidate for a neural correlate of pulse, perception, and temporal allocation of attention.

1. BACKGROUND & AIMS

The perception of pulse arises in response to musical rhythms that are organized around a (quasi) periodic temporal framework. In music, periodicities occur in the hundreds of milliseconds range. The behavioral significance of this time scale is well established: it is the range for detection of changes in tempo for periodic and nearly periodic sequences [1] and the rates for which anticipation is observed in sensorimotor synchronization tasks [2,3]. However, the cortical processes underlying the perception of pulse are still not well understood. One reason is that the time scale of music pulse is approximately the same as that over which low frequency event-related potentials (ERPs) unfold. Thus responses to individual stimulus events, recorded using noninvasive techniques, are difficult to resolve temporally [4,5].

Short latency auditory responses, originating in primary auditory cortex, are known to exist in the gamma-band (20-80*Hz*)[6]. These appear to be well suited for the study of rhythms that unfold on musical time scales. Evoked (phase locked) GBA is generally observed in response to tone onsets. Evoked GBA is well localized in time (generally lasting < 100*ms*)[6], its power does not diminish as tempo increases [7], and it is not observed during tone omissions [8]. Induced (non phase locked) GBA is anticipatory. Peaks in the power of induced gamma-band activity (GBA) predict both the timing and intensity of event onsets in metrically structured tone sequences. Moreover, the omission of individual events at expected times leaves the timing and power of induced GBA unchanged, as if an event had actually appeared [8]. These features of GBA match what is known about the perception of musical pulse. Here, we study the relationship between GBA and perturbations of isochronous tone sequences to investigate violations of temporal expectancy.

2. METHOD

2.1 Stimuli

Subjects were presented 262*Hz* sine tones with a total duration of 50*ms* and a rise time of 10*ms*. Sound stimuli were presented at a 500*ms* inter-onset-interval (IOI). Early, late, or on-time perturbations in the 500*ms* IOI baseline occurred every 6 to 10 tones (as shown in Fig. 1). Early and late perturbations of 125*ms* yield IOIs of 625*ms* and 375*ms*, respectively. The locus of perturbation (tone position 0) and perturbation type (on-time, early, or late) were randomized. The same randomized order was used for each subject. Subjects were presented 450 perturbed tones (150 perturbations for each of 3 conditions).

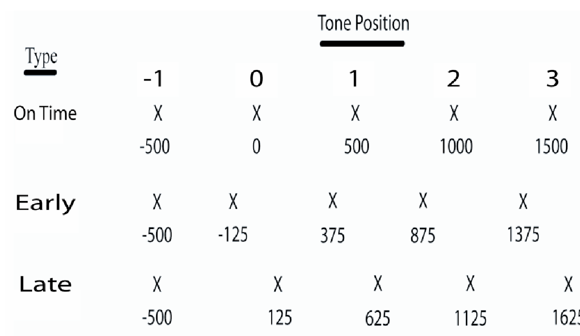

Figure 1: Stimulus sequences.

2.2 Subjects

8 right-handed subjects, 1 woman and 7 men (aged between 23 and 31, mean age = 28), participated in this study. Musical training ranged from 0 to 8 years for an average of 2.2 years. Subjects sat in a chair 3 feet in front of the speakers centered behind their head. Subjects were instructed to avoid body movements, and fixate their eyes on a cross on the wall in front of them.

2.3 Recording

EEG signals were recorded from 84 electrodes (Electro-Cap International, Inc., Eaton, OH) positioned according to the 10-10 method of placement and referenced linked mastoid electrodes with a right forehead ground. Ground and reference electrode impedances were maintained at <5*kΩ*, and recording electrodes at <10*kΩ*. The digitized EEG data was sent to a Pentium III Dell Dimension XPS T450 computer running Manscan 4.1 Microamps Recorder.

2.4 Data Analysis

Raw EEG data was bandpass filtered from .1-50*Hz* using a finite impulse response (FIR) filter. The filtered data were visually inspected for artifacts and 2 subjects were rejected because there were less than 80 artifact free trials per condition.

Data epochs began 300*ms* before the onset of tone –1 (see Fig. 1) and ended 300*ms* after tone 3. GBA was measured as follows. First, a time-frequency (TF) representation was computed for each epoch using a continuous 1-D complex Morlet wavelet transform (20-50*Hz*). This yields a two dimensional representation in which each point is represented by a complex number preserving both amplitude and phase information. Next we calculated evoked and induced GBA separately. The evoked response is calculated by averaging the TF representation over epochs and then calculating power. Evoked activity is observed when the fine time structure of the GBA is time locked to an event. The induced response was determined by first calculating power, and then averaging the TF representation over epochs. Induced activity is observed when the amplitude modulation of gamma activity (but not necessarily the fine time structure) is time locked to an event (for more details, see ref. 9).

Finally, we computed a summary TF representation for each subject by averaging over all electrodes. For both induced and evoked TF representations, individual frequencies from each subject were normalized over time using a vector normalization procedure. We then identified peaks in induced and evoked activity that occurred within +/-150*ms* of tone onsets. This yielded 5 GBA peaks (at tone positions *-1*, *0*, *1*, *2*, *3*) for each type of GBA (*induced* and *evoked*) and each perturbation condition (*early*, *on-time*, *late*), for each subject. We conducted two analyses of variance (ANOVAs) on the factors GBA (*induced*, *evoked*), perturbation (*early*, *on-time*, *late*) and tone position (*-1*, *0*, *1*, *2*, *3*). The dependent variables were latency (time of the peak relative to tone onset time) for the first ANOVA and peak power for the second ANOVA. To account for the shift in timing at the perturbed tone, we conducted an additional two ANOVAs on the same factors and DVs using a variable time window to identify peak activity (i.e. 100*ms* centered around tone onsets, -50/+175*ms* around early tones, -175/+50*ms* around late tones).

3. RESULTS

First, we quantified the latency of GBA peaks. We found a significant main effect of *induced* vs. *evoked* activity (repeated-measures analysis of variance (ANOVA), ($F(1,5) = 8.03$, $p < .05$; see Fig. 2). Induced peaks (mean latency = 3.6*ms*) preceded evoked peaks (mean latency = 18.4*ms*). This replicated an earlier finding [8] that induced GBA is anticipatory, reaching maximum power at about the same time as tone onset.

The second set of ANOVAs also turned up a significant three-way interaction between GBA, perturbation, and tone position ($F(4,8) = 2.22$, $p < .05$; see Fig. 3). Early tones resulted in longer latencies for both evoked and induced peaks. Induced activity around late tones peaks prior to tone onset and earlier than induced activity around on-time tones. Induced peak latency shows relaxation back to baseline in both the early and late perturbation conditions. This observed relaxation is similar to behavioral results on synchronizing with a perturbed metronome [10,11].

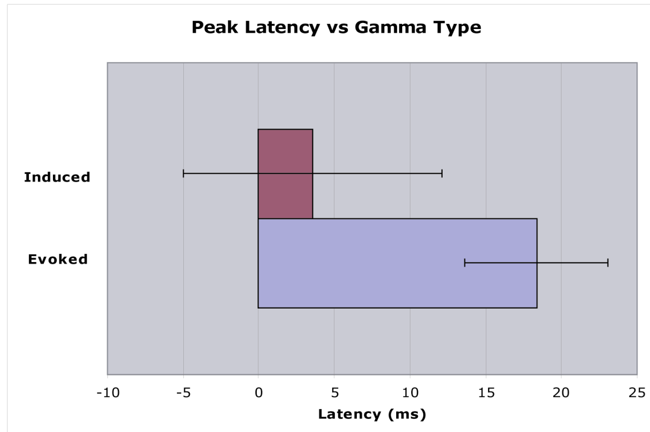

Figure 2: Induced peak latency (top) is earlier than evoked peak latency and is not significantly different from tone onset (0 ms).

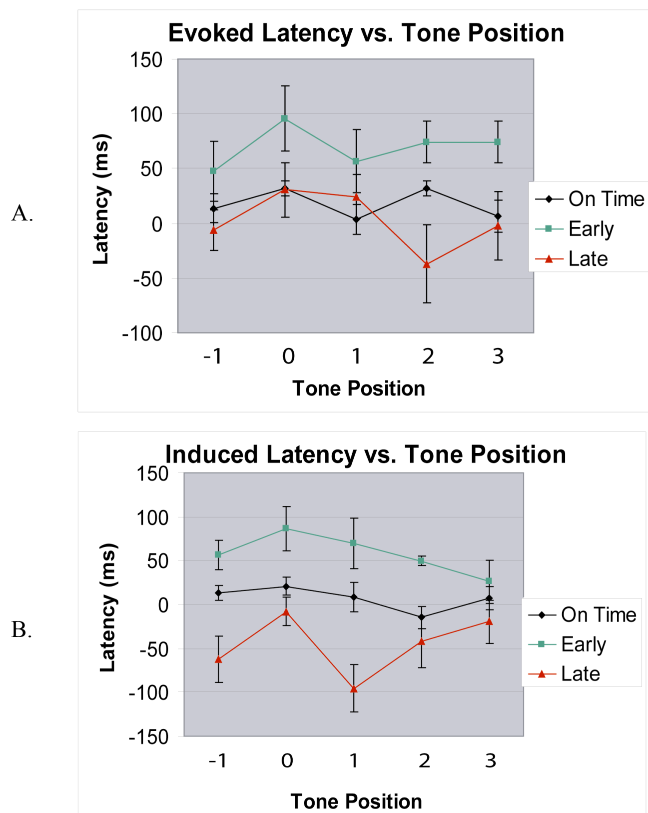

Figure 3: *A*. Early tones produce longer evoked peak latency. *B*. Early tones produce later peak induced responses while late tones produce earlier peak induced responses. Both perturbations yield relaxations back to baseline.

Next, we quantified the peak power of GBA. We found another significant three-way interaction between GBA, perturbation and tone position ($F(4,8) = 2.38$, $p < .05$). Peak power was greatest at the locus of the perturbation (i.e. tone 0) when tones were early.

The above results are summarized in Figure 4, which shows evoked and induced GBA, averaged over all subjects. Temporally regular evoked and induced activity can be seen in response to the isochronous stimulus (on-time condition; middle panels). Early tones produce an evoked peak approximately 20*ms* after stimulus onset and an *additional* evoked response 125*ms* after the early tone appeared (highlighted in the white box). This additional evoked response occurred approximately at the time the tone was expected to occur (dashed white line). Note also the diminished *induced* activity when tones occurred early. Late tones yield a typical induced response peaking around stimulus onset. However, an anticipatory induced peak (highlighted in a white box) occurs before the perturbed tone, shortly after where the tone was expected (dashed white line).

4. Conclusions

Our observations indicate that the observed cortical response to large perturbations is asymmetric. For early onsets, evoked peaks were observed to occur where the tone was expected. For late onsets, induced activity peaks where the tone was expected. Furthermore, the latency of induced peaks relaxes back to baseline after perturbations. Our results also confirm a distinction between induced and evoked auditory GBA and provide additional evidence supporting the role of induced GBA in temporal expectancy.

Metrical structures facilitate the production and memory of rhythm [12] as well as attention to individual acoustic events [13,14]. The predictable nature of metric rhythms produce an ideal environment for attention allocation [13,15]. The role of GBA in temporal expectancy is consistent with a range of findings regarding the significance of gamma-band processes in attention [8,16].

5. Acknowledgements

Research supported by NSF grant BCS-0094229 and NIMH grant MH42900.

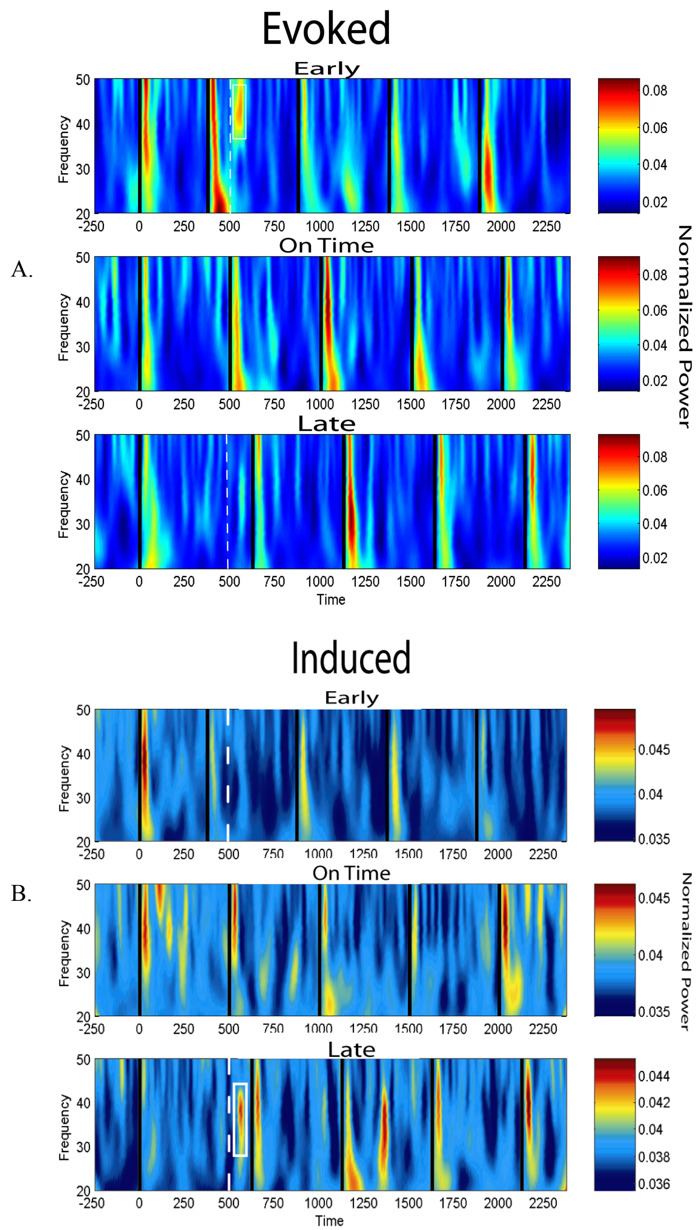

Figure 4: *A*. Early tones produce an evoked peak 20 ms after stimulus onset and another evoked response 125 ms after the perturbed tone (highlighted in a white box), where the tone was expected (dashed white line). *B*. Late tones yield a typical induced response peaking around stimulus onset and another induced response 125 ms before the perturbed tone (highlighted in a white box), again where the tone was expected (dashed white line).

6. References

1. Drake, C., & Botte, M. (1993). Tempo sensitivity in auditory sequences: Evidence for a multiple-look model. *Perception and Psychophysics*, 54, 277-286.

2. Mates, J., Radil, T., Müller, U. & Pöppel, E. (1994). Temporal integration in sensorimotor synchronization. *Journal of Cognitive Neuroscience,* 6, 332–340.

3. Engstrom, D.A., Kelso, J.A.S., & Holroyd, T. (1996). Reaction-anticipation transitions in human perception-action patterns. *Human Movement Science*, 15, 809-822.

4. Carver, F.W., Fuchs, A., Jantzen, K.J., & Kelso, J.A.S (2002). Spatiotemporal analysis of the neuromagnetic response to rhythmic auditory stimulation: rate dependence and transient to steady-state transition. *Clinical Neurophysiology*, 113, 1921-1931.

5. Desain, P. (2003). Listening to or imagining rhythms: An EEG study. *Rhythm Perception and Production Abstracts.*

6. Pantev, C. (1993). Relationship of transient and steady-state auditory evoked fields. *Electroencephalography and Clinical Neurophysiology*, 88(5), 389-396.

7. Snyder, J. S. & Large, E. W. (2004a). Tempo Dependence of Middle- and Long-Latency Auditory Responses: Power and Phase Modulation of the EEG at Multiple Time-Scales. (Manuscript under review).

8. Snyder, J. S. & Large, E. W. (2004b). Gamma-band activity reflects the metric structure of rhythmic tone sequences. (Manuscript under review).

9. Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Science, 3,* 151-162.

10. Repp, B. H. (2002). Phase correction in sensorimotor synchronization: Nonlinearities in voluntary and involuntary responses to perturbations. *Human Movement Science*, 21, 1-37.

11. Large, E.W., Fink, W., & Kelso, J.A.S. (2002). Tracking Simple and complex sequences. *Psychological Research*, 66, 3-17.

12. Large, E.W., & Jones, M.R. (1999). The dynamics of attending: how people track time varying events. *Psychological Review*, 106, 119-159.

13. Jones, M.R., Moynihan, H., MacKenzie, N., & Puente, J. (2002). Temporal aspects of stimulus driven attending in dynamic arrays. *Psychological Science*, 13, 313-319.

14. Driver, J., & Frith, C. (2000). Shifting baselines in attentional research. *Nature Review Neuroscience*, 1(2), 147-148.

15. Sakai, K., Hikosaka, O., et al. (1999). Neural representation of a rhythm depends on its interval ratio. *Journal of Neuroscience*, 19(22), 10074-10081.

16. Fell, J., Fernandez G., Klaver, P., Elger, C. E. & Fries, P. Is synchronized neuronal gamma activity relevant for selective attention? *Brain Res. Rev.* **42,** 265–72 (2003).