

Research report

Gamma-band activity reflects the metric structure of rhythmic tone sequences

Joel S. Snyder^{a,*}, Edward W. Large^b

^aDepartment of Psychology, Cornell University, Ithaca, NY 14853, USA

^bCenter for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL 33432, USA

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Abstract

Relatively little is known about the dynamics of auditory cortical rhythm processing using non-invasive methods, partly because resolving responses to events in patterns is difficult using long-latency auditory neuroelectric responses. We studied the relationship between short-latency gamma-band (20–60 Hz) activity (GBA) and the structure of rhythmic tone sequences. We show that induced (non-phase-locked) GBA predicts tone onsets and persists when expected tones are omitted. Evoked (phase-locked) GBA occurs in response to tone onsets with ~50 ms latency, and is strongly diminished during tone omissions. These properties of auditory GBA correspond with perception of meter in acoustic sequences and provide evidence for the dynamic allocation of attention to temporally structured auditory sequences.

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1. Introduction

Human auditory communication signals can be characterized as sequences of approximately discrete events, such as musical notes and speech syllables. *Rhythm* refers to the temporal patterning of such event sequences, especially the timing of events and the emergence of accent patterns. In music and speech, event onsets are perceived as being periodic with inter-onset intervals (IOIs) in the 100–1000 ms range. This time scale corresponds to the range over which humans are most sensitive to changes in tempo for periodic and nearly periodic sequences [6] and the rates for which anticipation is observed in sensorimotor synchroni-

zation tasks [7]. Rhythms that display multiple levels of periodic temporal structuring are called *metric rhythms*, and give rise to perception of alternating strong and weak accents [17,18]. Metric rhythms are easier to remember and reproduce than nonmetric rhythms [8], and result in characteristic patterns of functional brain activation [24]. Moreover, individual acoustic events are perceptually facilitated when presented in the context of metrically regular sequences [12,14]. Thus, attention may be allocated more efficiently to events as metric rhythms unfold in time, because they are more predictable [14].

Despite the significance of event timing in the perception of music and speech, no direct manifestation of metric expectancy for individual events has been reported in electroencephalography (EEG) or magnetoencephalography (MEG) recordings of human cortical activity. A recent study used an oddball paradigm to show that metrically strong beats in a sequence elicit a larger late response (~500 ms) possibly reflecting greater post-stimulus attention allocation [3]. However, it is likely that other aspects of meter

* Corresponding author. Rotman Research Institute, Baycrest Centre for Geriatric Care, 3560 Bathurst Street, Toronto, ON, M6A 2E1, Canada M6P2R6. Fax: +1 416 785 2862.

E-mail address: jsnyder@rotman-baycrest.on.ca (J.S. Snyder).

perception occur earlier, in anticipation of the occurrence of sounded events [12,14]. Moreover, given that alternating accents are characteristic of meter perception, we would expect to observe differential activity on strong versus weak beats within the metrical cycle.

Long-latency auditory responses have been studied extensively but are not typically studied at tempos characteristic of music and speech. This is in part because the responses diminish in amplitude at fast tempos and because responses from adjacent tone onsets begin to overlap at rhythmic rates with IOIs shorter than 1000 ms [5]. In contrast, short-latency evoked (phase-locked) gamma-band (20–60 Hz) activity (GBA) quickly follows stimulus events at a range of tempos [27], while induced (non-phase-locked) GBA can occur at various latencies and has been linked to integrative sensory, motor, and cognitive functions¹ [22,28]. The short latency and transience of auditory GBA suggests that it might underlie onset processing in auditory patterns, and we further hypothesized that it might underlie onset expectancy. The fact that induced GBA does not require precise phase locking to tone onsets suggests that it might exhibit activity prior to tone onset or around the time of missing tones. Such anticipatory activity is predicted by theories of meter perception that posit internal attentional processes that synchronize with external rhythmic patterns forming the basis of metric percepts [14], as illustrated in Fig. 1. Therefore, we investigated the relationship between evoked and induced GBA and the structure of metric rhythms in subjects while they listened to simple metrically structured tone patterns that included missing tones at strongly and weakly accented temporal positions.

2. Materials and methods

2.1. Subjects and procedure

Subjects were three male and five female subjects aged 24–45 who ranged in formal musical experience from none to university level music instructors. All subjects gave informed consent for the study. Review committees at Cornell University and Florida Atlantic University approved our study protocol. We delivered auditory stimuli using a graphical interface program written using MAX 3.6.2 (Cycling '74), running on a Macintosh G3 Powerbook. MAX sent musical instrument digital interface (MIDI) signals to an Akai S2000 synthesizer that converted the MIDI signals into tones. A Harmon/Kardon multi-media system consisting of two speakers approximately three feet behind the subjects delivered tones at a comfortable sound level. Auditory stimuli consisted of 262 Hz sine tones with

10 ms rise time and 40 ms steady-state duration. Subjects were asked to listen to the stimuli passively and were not given a task to control for vigilance. The experimenter made sure that subjects were able to stay alert by conversing with them between stimulus blocks. In all four conditions (see Fig. 1), subjects listened to multiple blocks with 60 tones in each block. In the *periodic control* condition (Fig. 1A), subjects listened to 300 uniform tones (5 blocks) presented at a constant rate of 390 ms IOI and with a constant MIDI velocity (proportional to intensity) of 70 (~50 dB SPL when adjusted to comfortable listening level). In the *binary control* condition (Fig. 1B), subjects listened to 300 cycles (10 blocks) of an alternating loud–soft accent pattern presented at the same IOI as the periodic condition. In this condition, the loud tones had a MIDI velocity of 100 (~55 dB SPL) and the soft tones had a MIDI velocity of 70, resulting in a binary subharmonic accent pattern. In the *omit-loud* condition (Fig. 1C), subjects listened to 1020 cycles (34 blocks) of the loud–soft accent pattern with occasional missing loud tones. Similarly, in the *omit-soft* condition (Fig. 1D), subjects listened to 1020 cycles (34 blocks) of the loud–soft accent pattern with occasional missing soft tones. In the omission conditions, approximately 30% of the cycles contained omitted tones with two constraints: (1) the first two cycles of a block could not contain omissions, and (2) no more than two cycles in a row could contain omissions.

2.2. EEG recording and analysis

We recorded neuroelectric signals on 84 channels from an EEG cap (Electro-Cap International) with linked mastoids as reference and ground placed on the forehead. Ground and reference electrodes impedance were maintained at <5 k Ω , and recording electrodes were <10 k Ω . A micro-amplifier amplified EEG signals before being digitized by a digital signal processor (Sam Technology, Inc.) that bandpass filtered the data (.05–100 Hz), sending the digitized signals (sampled at 256 Hz) to a Pentium III Dell Dimension XPS T450 computer running Manscan 4.1 (Sam Technology, Inc.) that recorded the data. A custom-designed micro-controller device received MIDI events and triggered tone-onset event marking on the computerized EEG record.

The EEG data were analyzed using custom MATLAB programs (MathWorks), running on a Macintosh G5 OSX workstation. We first bandpass filtered each block of data with a 25-point finite impulse response filter (15–100 Hz passband), using a zero-phase algorithm. Artifacts with activations exceeding a threshold of 20 μ V were excluded after bandpass filtering to remove muscle activations. We then calculated time-frequency (TF) representations of neural activity for each trial on each EEG channel, using a continuous wavelet transform (Matlab function *cwt.m*) with a complex Morlet wavelet family. The wavelet family was defined such that wavelet bandwidth was approximately 45% of f_c (*cmorl-1*), and f_c ranged from 20 to 60 Hz in 1 Hz

¹ Note that some studies define GBA as activity higher than 30 Hz, but for the purpose of measuring auditory evoked GBA, the more inclusive definition of 20–60 Hz we adopt here is more appropriate.

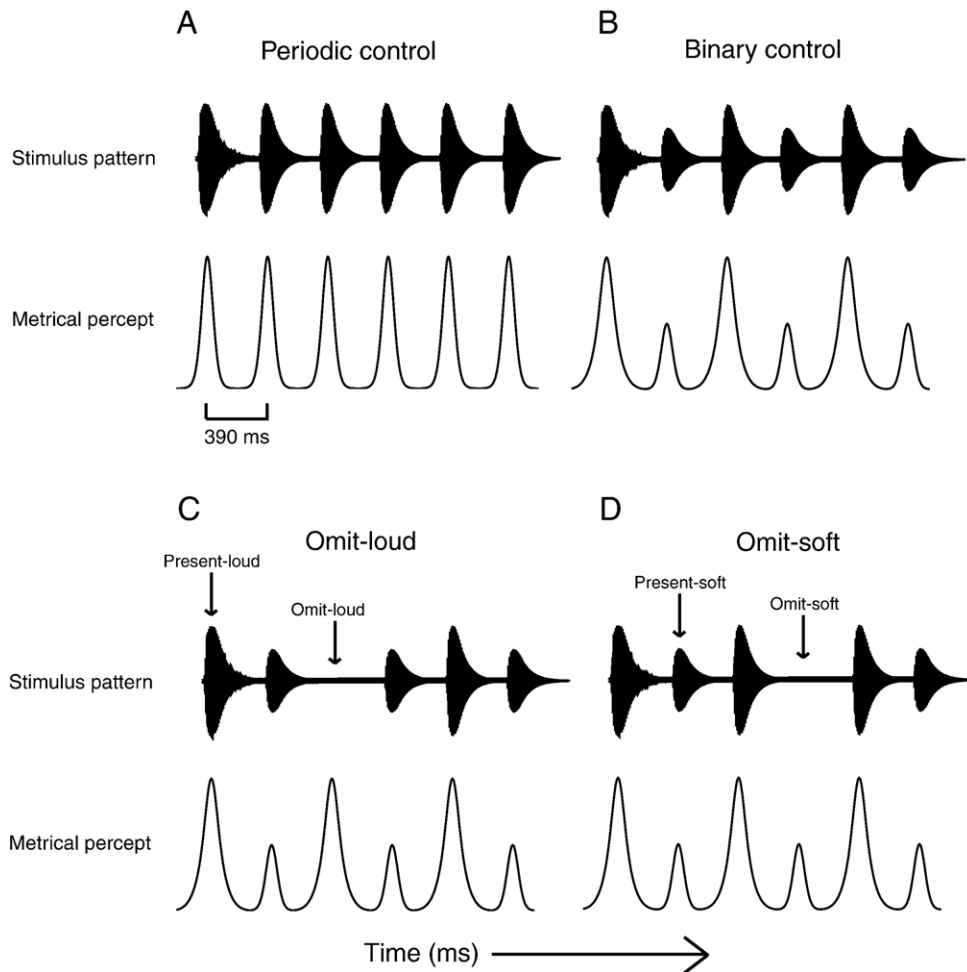


Fig. 1. Pure-tone (262 Hz, 50 ms duration) stimulus patterns are shown with inter-onset intervals of 390 ms (above) and schematized metrical accent representations (below). The *periodic control* condition consisted of isochronous tones designed to elicit a simple pulse perception (A). The *binary control* condition consisted of alternating loud and soft tones, designed to elicit a duplet meter perception (B). The *omit-loud* condition consisted of the binary control pattern with missing loud tones on 30% of two-tone cycles (C). The *omit-soft* condition consisted of the binary control pattern with missing soft tones on 30% of two-tone cycles (D).

steps. Fig. 2 illustrates how evoked and induced GBA was calculated from the TF representations. Briefly, *evoked* activity results from amplitude and phase modulation following tone onsets, whereas *induced* activity results only from amplitude modulation. For detecting tone-onset-locked responses, we averaged 780-ms sections of the TF representations (each containing responses to two tone onsets) with intervals beginning 195 ms before the onset of the first tone and ending 195 ms after the onset of the second tone. Grand averaged TF representations were means across all eight subjects and the 15 fronto-central channels (Fz, F1/2/3/4, FCz, FC1/2/3/4, Cz, C1/2/3/4). The TF representations depicted in figures only contain power and not phase information. Before peak analysis, we converted TF representations from power, P , in μV^2 to normalized power, P_{norm} , using the conversion: $P_{\text{norm}} = (P/P_{\text{min}}) / r_P$, where P_{min} is the minimum power and r_P is the range of power values for the TF representations of the corresponding recording blocks. This resulted in a range for

normalized power of $0 \leq P_{\text{norm}} \leq 1$, enabling comparisons across subjects and across conditions. We obtained values of peak normalized power, latency, and frequency of GBA for each of six stimulus types: periodic control, binary control, loud-present, loud-absent, soft-present, and soft-absent. We considered the peak to be the highest local peak in TF space within ± 195 ms of expected tone onset. We submitted the peak normalized latency and power values to repeated-measures analyses of variance (ANOVA) in SPSS.

3. Results

Fig. 3 shows one subject's non-normalized induced and evoked power in response to two identical tones (at 0 and 390 ms) in the periodic control condition for a subset of the 84 electrodes. We observed maximal activity at fronto-central electrodes for both types of GBA. We therefore measured induced and evoked power, averaged over 15

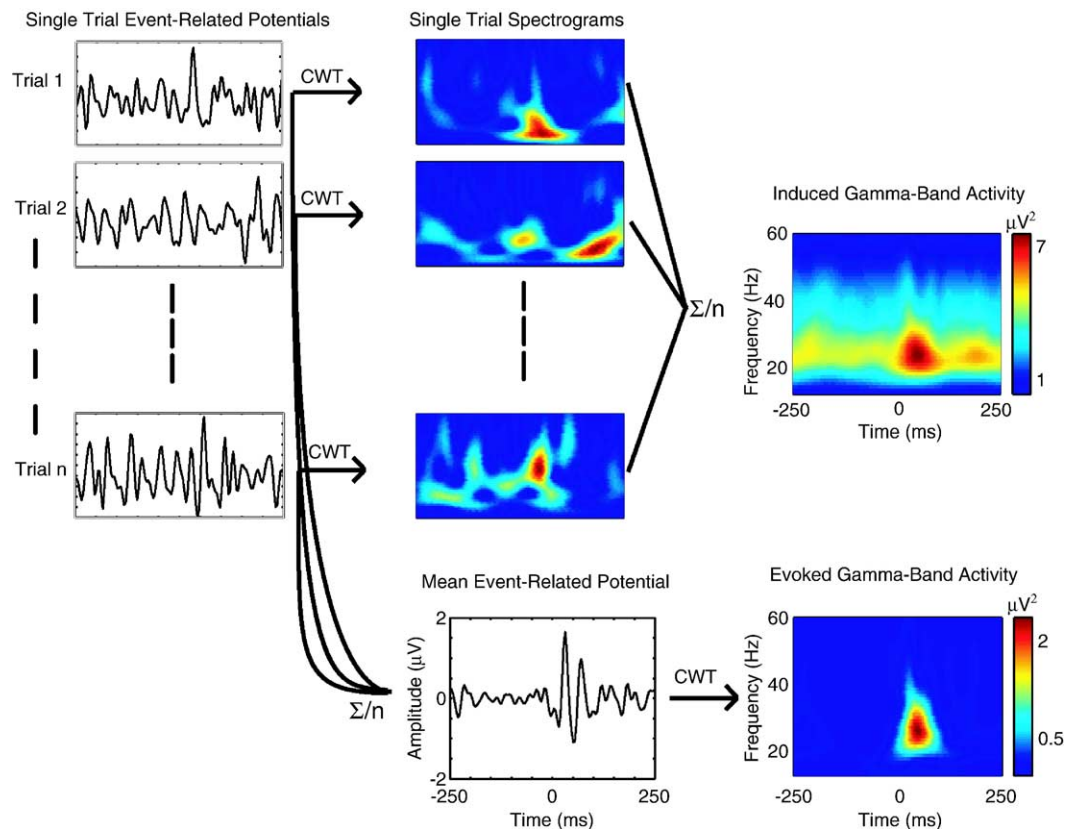


Fig. 2. Calculating evoked and induced gamma-band activity (GBA). Induced GBA requires taking the continuous wavelet transform (CWT) of each individual trial, and then taking the average power across trials without regard to phase. Evoked GBA requires first finding the mean event-related potential (ERP) across all trials and then taking the CWT of the ERP. In the current study, this was accomplished by averaging TF representations with both the amplitude and phase information present.

fronto-central electrodes, for each subject and each experimental condition. Fig. 4 shows mean TF plots, calculated as average normalized power across 15 fronto-central electrodes for induced and evoked GBA in the periodic control condition. All subjects demonstrated clear induced and evoked responses time-locked to tone onsets, although there was also substantial variation between subjects in the precise pattern of activation in TF space. Evoked GBA was generally observed to peak ~50 ms after tone onset. Additionally, some subjects showed unitary activations of GBA directly after tone onset (S2, S3, S4, S7, S8), whereas other subjects showed multiple activations (S1, S5, S6). Note that for one subject (S6), evoked GBA actually preceded tone onsets. Induced GBA occurred with transient peaks time-locked to tone-onset time. The induced activity for 2 subjects (S1, S7) in Fig. 4 preceded tone onset by more than 100 ms, whereas the other subjects showed maximal activity at or immediately after tone onset (at 0 and 390 ms). Moreover, in two subjects (S2, S7), induced GBA appeared to subdivide the interval, exhibiting four distinct peaks. Despite these between-subject differences, however, most subjects showed short-latency activations of evoked GBA following tone onsets with a marked tendency for induced GBA to precede evoked GBA. For some subjects, induced GBA preceded tone onset.

Fig. 5 shows induced and evoked GBA for three subjects in the binary control condition, in which a loud tone was presented at 0 ms and a soft tone at 390 ms. As in the periodic control condition, evoked GBA generally appeared following tone onsets with a latency of ~50 ms. Additionally, induced GBA occurred prior to evoked GBA. Evoked GBA showed a strong dependence on tone intensity with larger responses for the loud tones compared to the soft tones. Induced GBA appeared to show less of a dependence on intensity.

To statistically test the observations regarding latency and power, we compared type of GBA (induced vs. evoked) and tone intensity with peak latency and normalized peak power of the neural responses. Two separate ANOVAs were conducted on peak latency, one for the periodic control condition, and the other for the binary condition, which included the binary control condition and the cycles from the omit-loud and omit-soft conditions that did not contain omissions. The ANOVA for power also included the binary conditions. The results for the periodic control condition are shown in Fig. 6A. On average, induced GBA peaked earlier than evoked activity and before tone onset. This effect did not reach significance, however, $F(1,7) = 2.62$, $P = 0.15$, most likely due to the inter-subject variability of induced peak times (Figs. 4 and 6A). For the binary conditions,

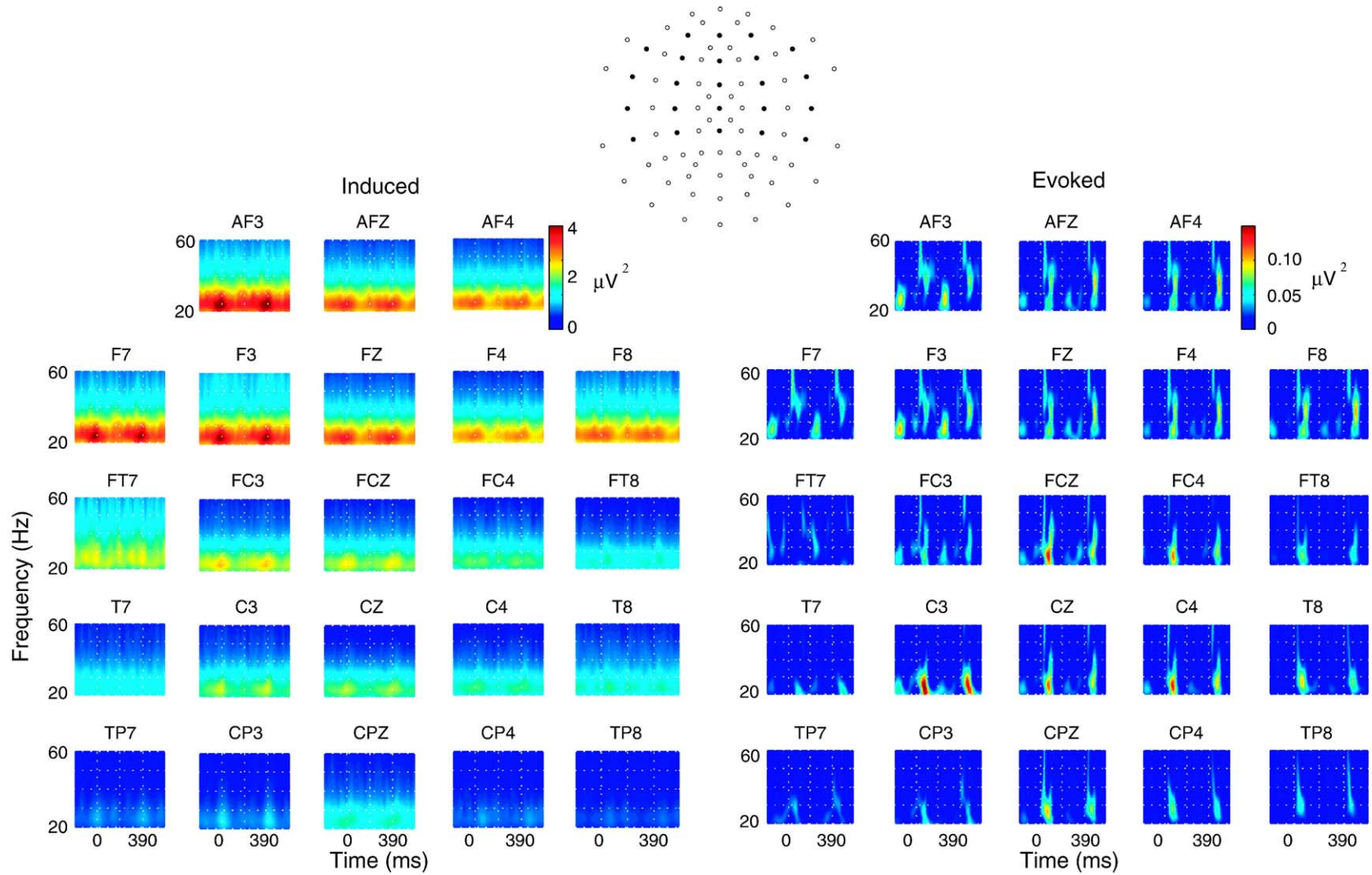


Fig. 3. Induced and evoked GBA for the periodic control condition with identical tones at 0 and 390 ms. Time-frequency (TF) plots of induced and evoked GBA for one subject (S3) at a subset of the 84 electrodes (positions indicated by dark dots in the electrode montage), showing the fronto-central distribution of power.

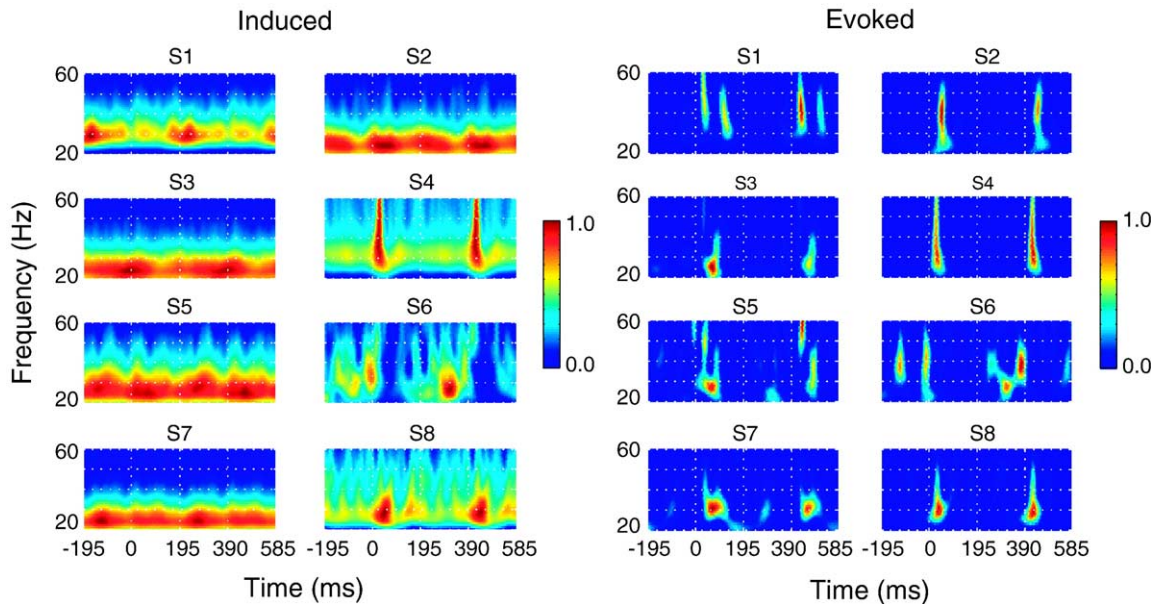


Fig. 4. Induced and evoked GBA for the periodic control condition with identical tones at 0 and 390 ms. Normalized plots of TF induced and evoked power as a mean across 15 fronto-central electrodes for each subject (S1–S8).

however, induced GBA peaked earlier than evoked activity, $F(1,7) = 5.83$, $P < 0.05$ (Fig. 6B), and the mean latency of induced GBA was not significantly different from 0 ms, $t(47) = 0.84$, $P = 0.41$. Again, some subjects' responses peaked prior to tone onset (see Figs. 3 and 4A). The latency for evoked activity, in contrast, was significantly larger than 0 ms, $t(47) = 10.83$, $P < 0.001$, confirming that induced GBA was more anticipatory than evoked GBA.

As shown in Fig. 6C, larger responses occurred following loud compared to soft tones, $F(1,7) = 21.19$, $P < 0.005$, reflecting a bottom-up representation of the simple binary metrical structure. This effect was most pronounced for the evoked GBA, although the interaction between tone intensity and GBA type was not significant, $F(1,7) = 3.85$, $P = 0.09$. Thus, evoked GBA occurs in response to

tones and shows a clear influence of tone intensity, with larger responses to loud tones. By contrast, induced GBA is anticipatory (at least for the loud tone) and does not strongly reflect tone intensity in its power.

Fig. 7 shows for three subjects induced and evoked activity when the loud tone (top) or the soft tone (bottom) was omitted. For the loud tone, the most striking commonality across subjects is that evoked GBA strongly decreased in power following tone omission (compare with Fig. 5), whereas induced power is largely preserved. Furthermore, omitting the loud tone reveals that activations of induced GBA begin before the time of expected tone onset in some subjects (S3, S8), supporting induced GBA as reflecting metrical expectancy. Interestingly, despite the strong diminution of evoked GBA following omission of the loud tones, some subjects showed residual activations (S3, S8) suggest-

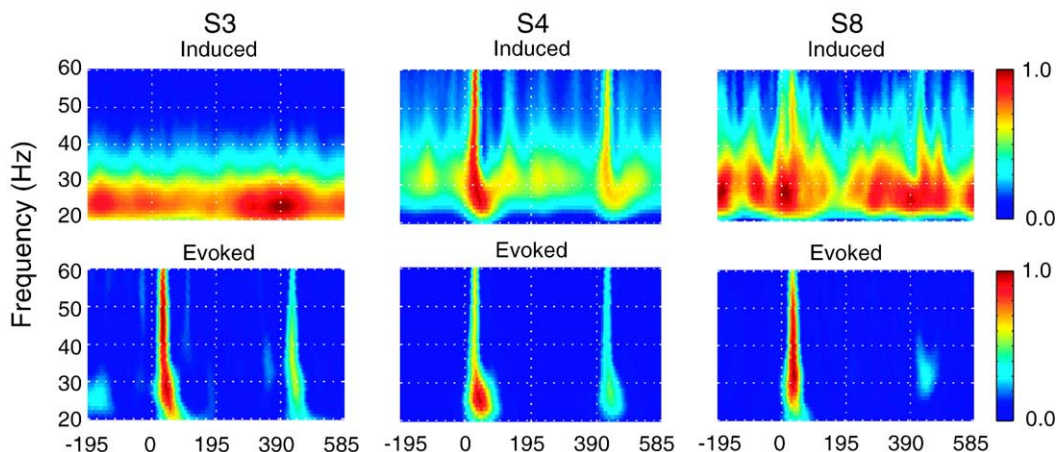


Fig. 5. Induced and evoked GBA for the binary control condition with loud tone at 0 ms and soft tone at 390 ms. Normalized plots of TF induced and evoked power as a mean across 15 fronto-central electrodes for three subjects (S3, S4, S8).

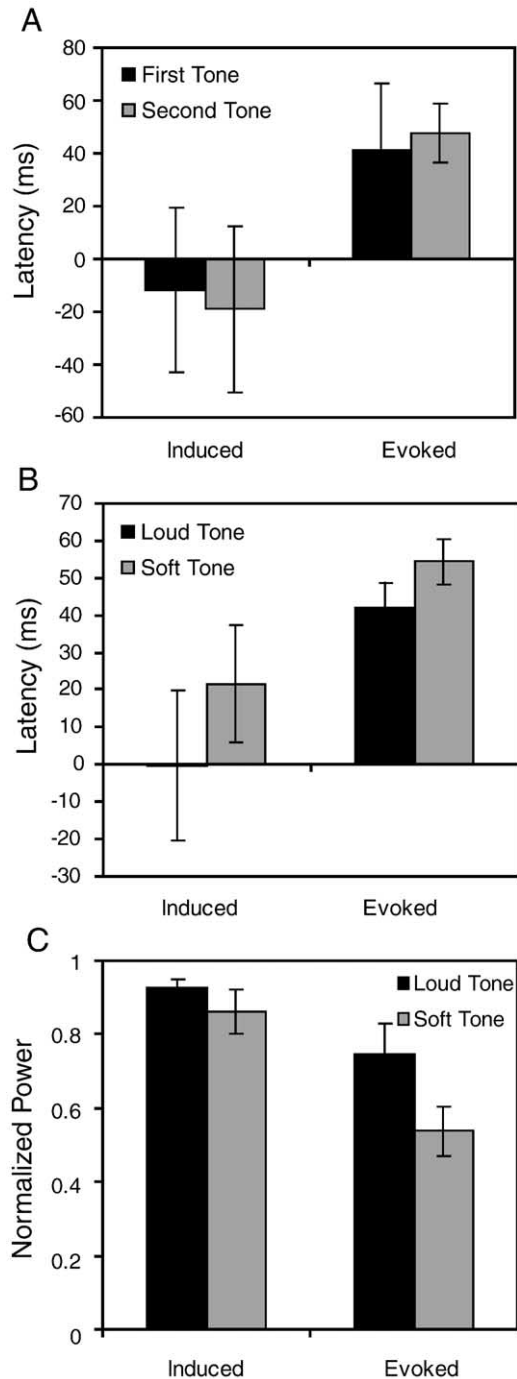


Fig. 6. Bar graphs showing mean (\pm SE) peak latency of induced and evoked power for the first and second tones in the periodic control condition (A), peak latency of induced and evoked power for the loud and soft tones across the binary control, omit-loud, and omit-soft conditions (B) and peak normalized induced and evoked power for the loud and soft tones across the binary control, omit-loud, and omit-soft conditions (C).

ing that even high-frequency phase-locked brain activity can display expectancy properties. Similarly, for omissions of the soft tone, evoked GBA was strongly diminished, while induced GBA showed preserved activations.

Fig. 8A summarizes the above observations, showing TF plots of induced and evoked GBA in the binary control

(left), omit-loud (middle), omit-soft (right) conditions as a grand-mean across the eight subjects. When the loud tone or soft was absent, preservation of induced GBA can be seen compared to the binary control condition. Evoked GBA, on the other hand, was strongly diminished, although some residual activity is visible. This is confirmed by significant reductions in power following omitted loud tones, $F(1,7) = 5.70$, $P < 0.05$, and omitted soft tones, $F(1,7) = 10.19$, $P < 0.01$, and an interaction between GBA type and presence/absence of the tones on peak power for the loud tones, $F(1,7) = 13.40$, $P < 0.01$ (Fig. 8B). The corresponding interaction for the soft tones was not significant, $F(1,7) = 3.10$, $P = 0.12$.

4. Discussion

For the metrical rhythms of this study, peaks in the power of GBA predicted both the timing and intensity of event onsets; meanwhile, the omission of individual events at expected times left the power of induced GBA largely unchanged. These features of induced activity closely match what is known about the perception of auditory sequences, including anticipation of events [7], sensitivity to metrical structure [9,14,26,29], and persistence of metrical representation [15,21]. Thus, our findings have important implications for the understanding of rhythm perception, by providing evidence for early auditory processing underlying metrical expectancy [12,14]. A recent study found neuroelectric correlates of metrical processing by presenting uniform metronome tones that were presumed to give rise to a perception of alternating accents, a phenomenon termed *subjective accent* [3]. These authors found late neuroelectric responses that were larger for strongly versus weakly accented tones having intensity decrements. Such late responses might reflect a post-tone-onset facilitation of perceptual discrimination dependent on metrical accent, whereas the present study showed metrical differentiation in neural activity occurring at the time listeners were expecting tone onsets to occur. Thus, anticipation of temporally structured acoustic sequences may facilitate later stages of processing including perception and memory.

The current study replicates and extends previous studies of auditory emitted potentials, neuroelectric responses to omissions of expected sounds. As in the current study, previous findings showed that omitting a sound in an otherwise isochronous train of sounds elicits brain responses similar to when the sound was physically present [1,2,10,13,20,23,25]. Short-latency emitted potentials that are similar to sensory evoked responses likely represent neural activity in anticipation of sensory processing. In contrast, longer-latency emitted potentials might represent an oddball response following the violation of temporal expectancy [1,10,13]. The present study extends previous findings by demonstrating that induced high frequency often precedes the onset of expected events, generally precedes

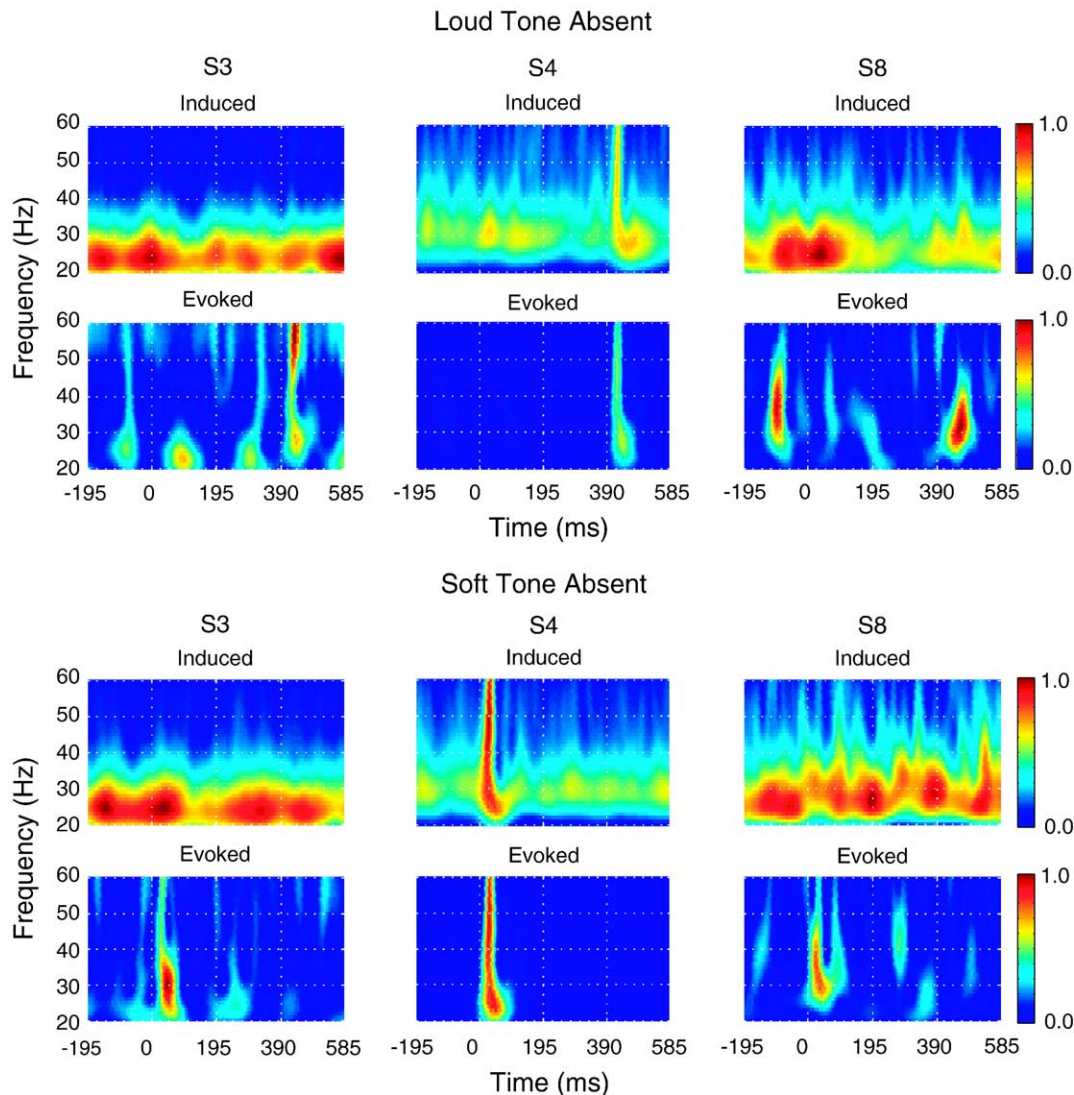


Fig. 7. Induced and evoked GBA for tone omissions. The omit-loud (top) condition contains an absent loud tone at 0 ms and a present soft tone at 390 ms with normalized plots of TF induced and evoked power as a mean across 15 fronto-central electrodes for three subjects (S3, S4, S8). The omit-soft (bottom) condition contains a present loud tone at 0 ms and an absent soft tone at 390 ms.

evoked activity, and is observed even when expected sounds are omitted. The current findings further showed that emitted potentials show specificity to the metrical position of the expected sound. Some subjects additionally showed evoked activity following tone omissions, demonstrating precisely phase locked high-frequency activity, thus revealing extremely precise timing of neural activity in anticipation of sensory events.

Anticipatory cortical activity is consistent with a range of neurophysiological findings using methods besides emitted potentials. Well-studied cases include slow potentials that precede sensory or motor events [4]. Increased brain activity in anticipation of expected stimulation may reflect a modality-general property of the nervous system that arises from communication between neural ensembles. Such activity may play a role in processing rapidly evolving temporal patterns such as music and speech, in which it is

important to develop forward-looking representations for when events are likely to occur [16]. This is consistent with the notion of an attentional process that primes perceptual responses for temporally predictable stimulus contexts [12,14]; the fact that these processes can be observed in GBA is also consistent with a range of findings regarding the significance of GBA in attention [28]. The ability to detect anticipatory brain events using a direct and objective measurement could allow the study of temporal pattern processing in infants or other populations that cannot participate in the complex perceptual and sensorimotor tasks that are often used to test adult human subjects [9,15,26,29].

In the current study, we found induced and evoked activity that occurred following tone onsets and induced activity following tone omissions. The induced activity varied more between subjects than evoked activity in the

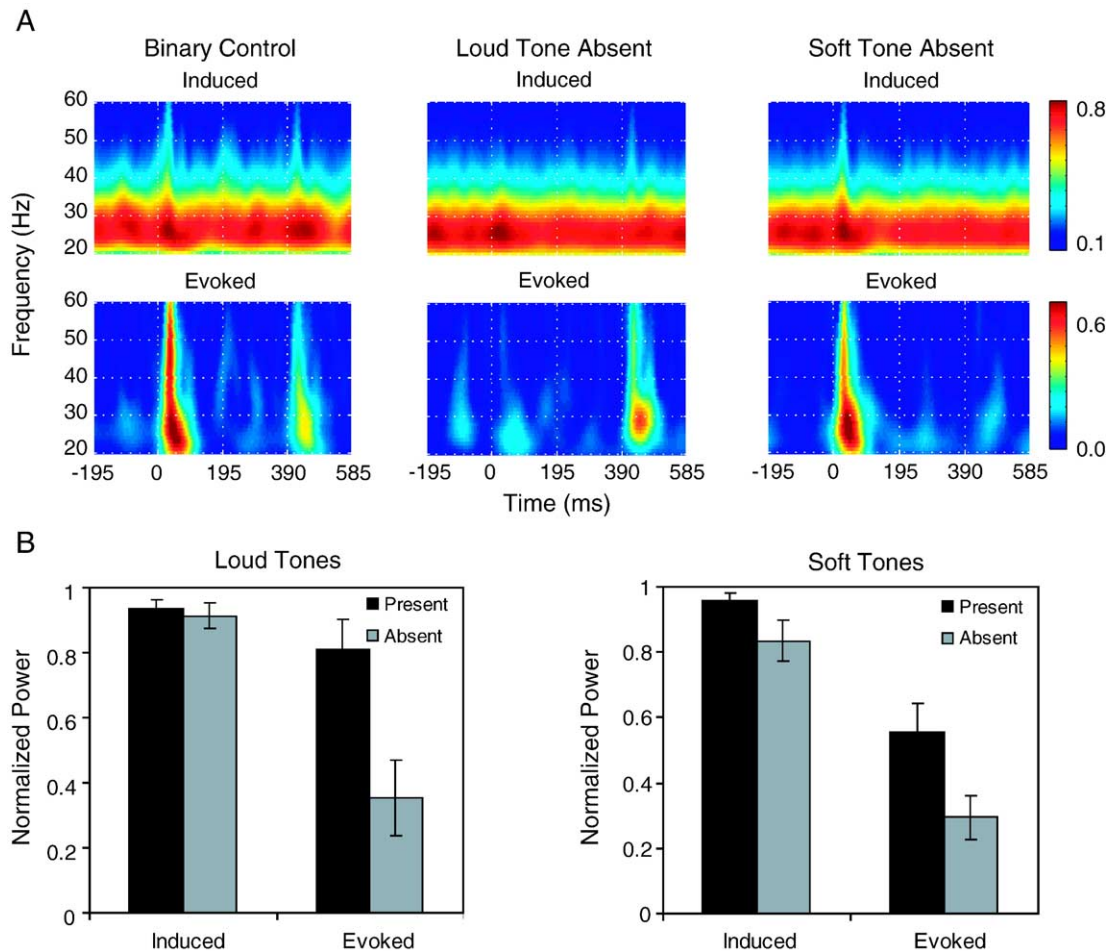


Fig. 8. Grand-mean evoked and induced power for tone omissions. Grand-mean ($N = 8$) normalized plots of TF induced and evoked power for the binary control, omit-loud, and omit-soft conditions (A). Bar graphs showing mean (\pm SE) induced and evoked power for present and absent loud (left panel) and soft (right panel) tones (B).

timing relative to tone onsets and the extent to which it exceeded the background activity. Such variability might be explained by individual differences in attention during the task, musical experience, and listening strategies, especially in the more rhythmically complex stimulus conditions. A number of previous experiments have elicited transient GBA suggesting a general role in auditory perception [22]. In humans, when one click followed another by more than 12.5 ms (the approximate threshold for perceiving two distinct events), the second click reset the phase of evoked GBA suggesting a role in limiting temporal resolution [11]. The current findings suggest that auditory GBA might play a role in developing temporally precise, intensity-specific neural expectations for complex, temporally structured tone sequences. Given the large variability in responses across subjects, however, this hypothesis should be explored in future studies. Further evidence for this interpretation could come from correlating performance on rhythm perception tasks such as synchronization tapping [7,15,26,29], rhythm reproduction [8], or tempo discrimination [6] with induced GBA. For example, recent findings showed larger late responses to tone

omissions in drummers and bass guitarists compared to non-musically-trained individuals [13].

Our results demonstrate that induced GBA precedes evoked GBA, implicating a functional relationship between the two: induced GBA increases might predict events, and the occurrence of the tone onset evokes a phase-locked gamma-band response. This would be consistent with previous reports that evoked responses represent the modulation of ongoing EEG activity rather than the transient activation of neuronal populations [19]. Thus, the anticipatory increases of induced GBA may result in a larger and/or more synchronized population of neurons contributing to EEG phase resetting.

In summary, we found that high-frequency auditory activity occurring around the time of tone onsets both reflects stimulus-driven and expectancy-based representations of a simple binary metrical structure. Induced activity showed activations that in some cases preceded tone onsets and showed very little diminution with omissions of expected tones. Evoked activity, on the other hand, showed a much stronger dependence on the physical presence of tones with larger responses to loud than soft tones and large

diminution with tone omissions. These findings support current theories of meter perception that posit an active expectancy-based processing [14], and demonstrate the potential usefulness of short-latency auditory neuroelectric responses for studying processing of rapid temporal patterns such as ongoing speech and music.

Acknowledgments

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