Gamma-Band Responses to Perturbed Auditory Sequences: Evidence for Synchronization of Perceptual Processes

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We measured modulations of neuroelectric gamma-band activity (GBA) as subjects listened to isochronous pure-tone sequences with embedded temporal perturbations. Perturbations occurred every 6–10 tones, and at the locus of the perturbation, tones occurred early, on time, or late. In the absence of perturbations, induced (non–phase-locked) GBA reached maximum power simultaneously with the occurrence of tone onsets, whereas evoked (phase-locked) GBA peaks were observed after onsets. During late perturbation trials, peaks in induced activity tended to precede tone onsets, and during early perturbation trials, induced peaks followed tone onsets. Induced peaks returned to synchrony after both types of perturbations. Early tones resulted in a marked increase in evoked GBA power at the locus of the perturbation. The latency of evoked GBA relative to tone onset, as well as some other features of the response, depended asymmetrically on the direction of the perturbation. The current results provide evidence for the synchronization of GBA during the perception of auditory rhythms, thus supporting the role of GBA in temporal expectancy.

Tʜᴇ perception of pulse is fundamental to the perception of musical rhythm. Listening to music almost invariably gives rise to the perception of a pulse, or musical beat, and studies of music perception have characterized pulse as a series of temporal expectancies for auditory events. Expectancies are thought to be generated whether or not acoustic events are actually presented at expected times (Cooper & Meyer, 1960), to occur synchronously with event onsets, and to be well-localized in time

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(Lerdahl & Jackendoff, 1983; Large & Jones, 1999). Because the perception of pulse arises in response to rhythms that are organized around a (quasi) periodic temporal framework, and are therefore predictable, it has been postulated that the generation of temporal expectancies reflects an optimal allocation of attention to acoustic events as rhythms unfold in time (Large & Jones, 1999). This proposal has received support from studies that have shown that individual events are perceptually facilitated when presented in the context of temporally regular sequences (Large & Jones, 1999; Jones, Moynihan, MacKenzie, & Puente, 2002).

In music, the periodicities that give rise to pulse perception occur on the time scale of hundreds of milliseconds (see, e.g., van Noorden & Moelants 1999), and this time scale has been shown to have behavioral significance. People are most sensitive to changes in the tempo of periodic and nearly periodic sequences in this range, with best detection accuracy at approximately 600 ms (Drake & Botte, 1993). In sensorimotor synchronization tasks, anticipation is observed for periodic sequences in this range (Mates, Radil, Muller, & Poppel, 1994; Engström, Kelso, & Holroyd, 1996). Moreover, when asked to synchronize taps with complex rhythms, people generally choose the periodicity nearest 500 ms (Handel, 1981; Van Noorden & Moelants, 1999; Snyder & Krumhansl, 2001), and this preference has been modeled using models of both linear (Todd, Lee, & O'Boyle, 1999) and nonlinear (Large, 2000) resonance.

The ability to coordinate motor behaviors with periodic auditory stimuli has been widely studied because motor responses provide readily observable, on-line measures of synchronization (Bartlett & Bartlett, 1959; Dunlap, 1910; Fraisse, 1956; Kohlers & Brewster 1985; Michon, 1967; Stevens, 1886; Vos, Mates, & van Kruysbergen, 1995; Woodrow, 1932). In particular, temporal perturbation methodologies provide the means to observe sensorimotor anticipation and error correction (Michon, 1967). For example, Repp (2002a) observed a phase correction response when tapping to a perturbed metronome, and Vorberg and Wing (1996) modeled sensorimotor synchronization in response to perturbations. It has further been proposed that pulse is an inherently sensorimotor phenomenon such that pulse perception necessarily involves motor system activity (Todd et al., 1999). However, it is difficult to directly compare perceptual and motor experiments. Sensorimotor synchronization experiments yield periodic movements that can be directly measured. Perceptual/attentional approaches rely on perceptual judgments, which are then used to infer the existence of pulselike representations, presumably involving periodic neural activity.

As a first step toward distinguishing between these possibilities, it makes sense to attempt to observe neural activity as subjects listen to rhythmic sequences without making overt motor responses. Unfortunately, the relationship between neural activity and rhythm per-

ception has proven difficult to resolve. One reason is that musical pulse and long latency responses (LLRs) occur over the same time scale. LLRs are products of large neuronal populations synchronously firing at a set time in response to a stimulus and have been shown to last 500 ms or more after stimulus onset (Basar-Eroglu, Basar, Demiralp, & Schurmann, 1992; Carver, Fuchs, Jantzen, & Kelso, 2002; Johnstone & Barry, 1999). Carver et al. (2002) presented tones binaurally at 27 different stimulation rates from 0.6 to 8.1 Hz (1667ms–123ms). Over this range, they observed a transition between a transient evoked response at low frequencies and a continuous steady-state response at high frequencies. They show that it is the onset of temporal overlap between responses to successive tones that leads to this transition, which is preceded by the diminution of the N100 (a negative component of the LLR). These effects are already clearly observable at rates of 500–600 ms, the most important range for pulse perception. Indeed, noninvasive recording techniques have difficulty distinguishing responses to individual stimulus events. Thus, at rhythmic time scales, it has not been possible to distinguish activity in response to a preceding event from activity that anticipates an upcoming event.

Auditory mid-latency responses (MLR), originating in primary auditory cortex, are known to exist in the gamma (20–80 Hz) range (Pantev et al., 1991). These appear to be well suited for the study of rhythms that unfold on musical time scales (Snyder & Large, 2004, in press). There are two types of gamma-band responses, *evoked* and *induced*. The distinction depends on how the gamma activity is time-averaged, as illustrated in Figure 1. Panel A shows two sets of trials, temporally aligned with respect to a hypothetical stimulus. Both depict bursts of 40-Hz activity peaking at the same time with respect to the stimulus. The left panel illustrates gamma bursts of different phases, in the right panel, the phase of each response is nearly the same. Panel B shows the result of time-averaging the two sets of trials. On the left, a minimal response is registered, whereas on the right a strong response in indicated. This sort of averaging leads to an evoked response. Hence, an evoked response is registered only when the phases of gamma oscillations are time-locked to the stimulus event. However, this misses the amplitude peaks in the non–phase-locked gamma activity. We can register these peaks if we calculate the signal envelope before averaging (Panel C). This registers a response when amplitude peaks are time-locked to the stimulus, ignoring the phase of the gamma oscillations. In other words, an evoked response is observed when gamma oscillations are phase-locked to a stimulus, and an induced response is observed when peaks in gamma activity are time-locked to a stimulus.

In this study, we examine both evoked and induced responses. Evoked (phase-locked) GBA is observed in response to tone onsets, and it is well localized in time such that the gamma-band response generally lasts less than 100 ms (Pantev et al., 1991). Snyder and Large (2004) measured

A. Individual Trials

B. Average Waveforms

C. Average Envelope
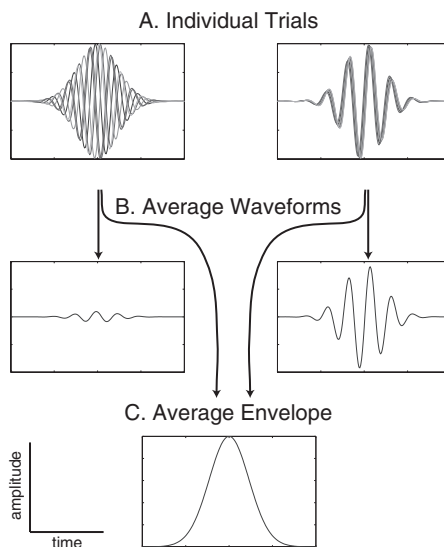
Fig. 1. Distinction between evoked and induced gamma-band activity (GBA). (A) Two examples of gamma bursts superimposed over several hypothetical trials. The bursts on the left have variable phase; the bursts on the right have similar phase. Both peak at the same time. (B) Averaging over trials is equivalent to the calculation of the evoked GBA. (C) Induced GBA relies on the average envelope of the gamma bursts, thereby retaining the non–phase-locked activity.

both mid-latency and long latency auditory responses to pure-tone patterns at 10 different tempos from 150 ms to 3125 ms. They observed a decrease in the N100 LLR as tempo increases, whereas evoked gamma-band activity retained a consistent level of power across all tempos. In a second study, peaks in the power of induced (non–phase-locked) GBA were found to predict both the timing and intensity of event onsets. Moreover, the omission of individual events at expected times left the timing and power of induced GBA unchanged (Snyder & Large, 2004). These characteristics of induced activity appear to match what is known about the perception of auditory sequences, including anticipation of events (Engström et al., 1996; Mates et al., 1994), sensitivity to structure (Large & Jones, 1999; Snyder & Krumhansl, 2001), and persistence of metrical representations (Palmer & Krumhansl, 1990; Large, Fink, & Kelso, 2002).

These observations suggest that the distinction between evoked activity and induced activity is behaviorally significant, with induced activity indexing expectancy and evoked activity indexing reactions to sounded events. Thus GBA may play an important role in the perception of rhythmic tone sequences with tempos typical of music. In this study, we seek to

investigate neural correlates of pulse perception in auditory sequences. In particular, we investigate the role of evoked and induced gamma-band activity. Based on previous findings, we expect to observe evoked GBA in response to tone onsets, whereas induced GBA may anticipate tone onsets. We induce an expectation of simple periodic structure through isochronous tone sequences. Using temporal perturbations, we observe neuroelectric activity as temporal expectations are violated and reestablished.

Methods

STIMULI

Sound stimuli are shown in Figure 2. Pure tones (50-ms total duration, 10-ms rise time) were presented at a 500-ms interonset interval (IOI). Temporal perturbations were inserted randomly, every 6–10 tones. At the locus of the perturbation, tones occurred early (-125ms), late (+125ms), or on time (0 ms; i.e., no perturbation). Perturbation type was also randomized, and the same randomized sequences were presented to every subject. Subjects were presented a total of 450 perturbed tones (150 perturbations for each of the three types). Musical instrument digital interface (MIDI) stimuli were generated by using Max 3.6.2 running on a Macintosh G3 Powerbook. An Akai S2000 generated the tones, and the stimulus was presented through a Peavey RQ 200 mixing board and Harmon/Kardon speakers. The intensity of the sound stimulus was adjusted to a comfortable listening level.

SUBJECTS

Eight right-handed subjects, one woman and seven men (between 23 and 31 years old, M = 28 years), participated in this study. Musical training ranged from 0 to 8 years with an average of 2.2 years. Subjects sat in a chair 1 m (3 ft) in front of a pair of stereo speak-
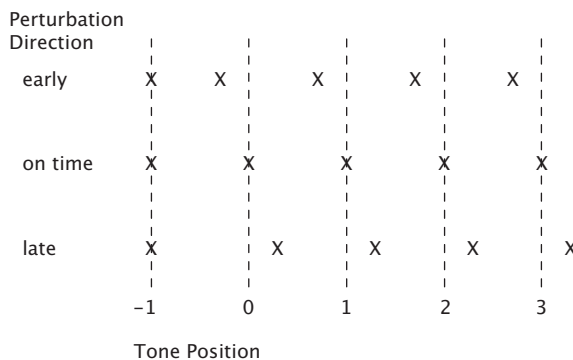

Fig. 2. Stimuli for the perturbation experiment. "X" represents tone onset, and indices mark position relative to the perturbed tone. ~~The on-time condition displays the 500-ms interonset interval, whereas the early and late conditions show a perturbation at Tone 0.~~ One epoch consisted of five tones, beginning 300 ms before Tone -1 and ending 300 ms after Tone 3.

ers positioned behind their head. Subjects were instructed to avoid body movements and fixate their eyes on a cross on the wall in front of them.

RECORDING

Electroencephalographic (EEG) signals were recorded from 84 electrodes (Electro-Cap International, Inc., Eaton, OH). The electrodes were positioned following the 10-10 method of placement and were referred to linked mastoid electrodes with a right forehead ground. Ground and reference electrode impedances were maintained at <5kΩ and recording electrodes were <10kΩ. A Microamp amplifier and digital signal processor (Sam Technology, Inc., San Francisco, CA) with a sampling rate of 256Hz and a frequency response of 0.01–100Hz processed the EEG signal. The digitized EEG data were sent to a Pentium III Dell Dimension XPS T450 computer running Manscan 4.1 Microamps Recorder. Stimulus onset and offset signals generated by the Macintosh G3 Powerbook were sent to a Mark of the Unicorn (MOTU) Micro Express USB MIDI interface and then to a custom-designed microcontroller. From the microcontroller, all stimulus onsets and offsets were synchronized with the EEG data via the digital signal processor.

DATA ANALYSES

Raw EEG data were band-pass filtered from 0.10 to 50Hz using a finite impulse response filter. The filtered data were visually inspected for artifacts, and two subjects were rejected because they had fewer than 80 artifact-free trials per condition. Individual trials began 300 ms before the onset of Tone "-1" (i.e., the tone before the perturbation, see Figure 2) and ended 300 ms after Tone 3. Event-related potentials (ERPs) were obtained for each subject by averaging all trials for each electrode. The N100 response (a long-latency negative component of the ERP) was identified as the largest local minima observed between 50 and 150 ms after the stimulus.

Gamma-band activity (GBA) was measured as follows. First, a time-frequency (TF) representation was computed for each trial at each electrode using a continuous one-dimensional 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. Evoked and induced GBA were then calculated separately. The evoked response was calculated by averaging the TF representations over trials and then calculating power. This method preserves the phase of the gamma-band activity, thus evoked responses are only observed when the fine time structure of the GBA is time locked to an event. By contrast, the induced response was determined by calculating power before averaging the TF representation over trials. This method eliminates the phase of the gamma-band activity before averaging, thus induced activity is observed whenever amplitude modulation of gamma activity is time locked to the stimulus (Tallon-Baudry & Bertrand, 1999). Because the power in EEG recordings falls off as $1/f$, power at each electrode was normalized over each frequency band such that $\int_t^T x(t, f)^2 = 1$. This normalization procedure also enhances peaks in the signal.

Results

LONG LATENCY RESPONSE

Time series of the ERPs are shown for S6, channel CZ, in Figure 3. The solid vertical lines represent tone onset, and dashed vertical lines denote an expected tone. Early tones (Panel A) produce a large negative peak around 150 ms, 50 ms later than a typical N100 response (Näätänen &
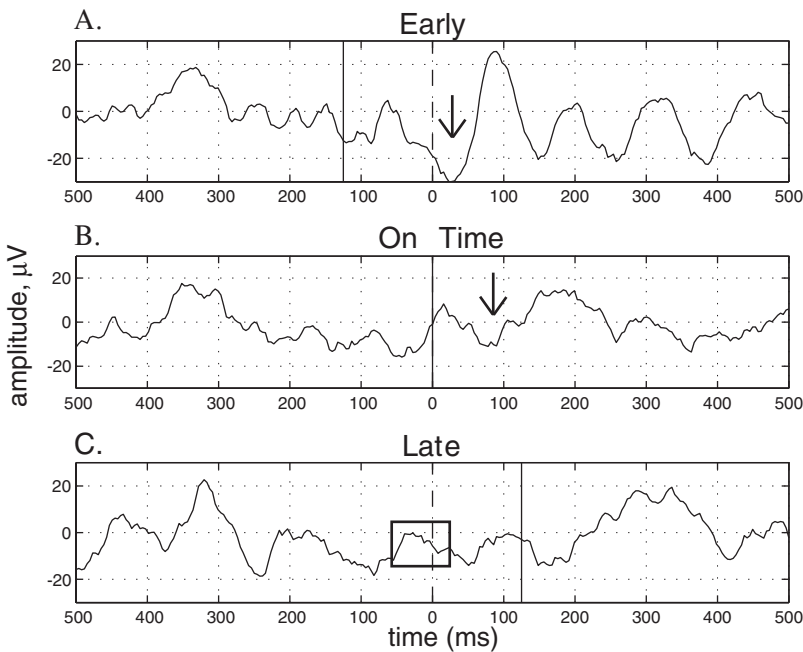
Fig. 3. Event-related potential (ERP) time series for each condition, S6, channel CZ. Time is shown relative to when the tone was expected (dashed line). (A) Early: There is a delayed N100 (arrow) compared with late and on-time tones. (B) On-time: A typical latency of the N100 response can be seen (arrow). (C) Late: The box highlights a low-frequency ERP component, peaking near the expected tone onset. A diminished P30 is present along with a stronger P50 response.

Picton, 1987). On-time tones (Panel B) evoke an N100 response at a more typical latency of about 100 ms. Moreover, a suppressed 50 ms positive component (P50) and an enhanced 30 ms positive component (P30) are evident. Carver et al. (2002) provide evidence that the enhanced P30 results from an overlap of a 500-ms low-frequency ERP component (due to the previous tone) with the P50 when stimulated at 2 Hz (500-ms IOI). The late condition (Panel C) demonstrates a 500-ms ERP component (highlighted in the box) that peaks near the expected tone onset. This late positive component dissuaded us from an analysis of LLRs for a possible anticipatory element.

Two two-way analyses of variance (ANOVA) were conducted on channel CZ's N100 response with the factors perturbation type (early, on time, late) and tone position (-1, 0, 1, 2, 3). The dependent variable for the first ANOVA was peak latency of the N100. The dependent measure for the second analysis was peak amplitude. The latency analysis showed a two-way interaction of perturbation type and tone position, $F(8,40) = 3.71$, $p < .01$ (Figure 4a). Similarly, the amplitude analy-
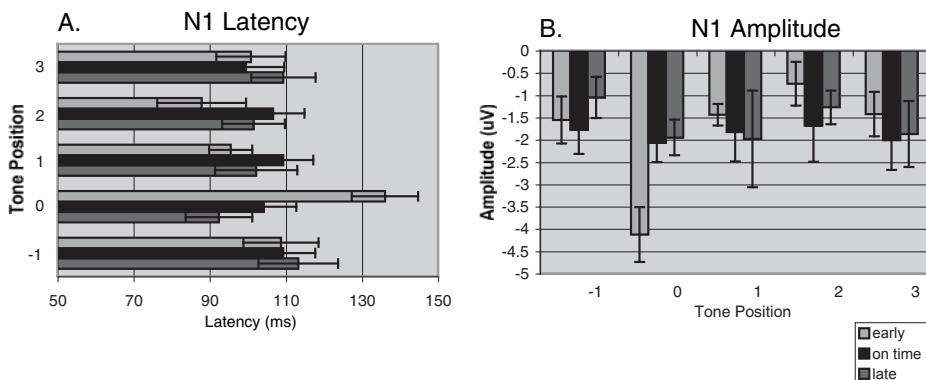
Fig. 4. Channel CZ's N100 response for each tone position and condition. Early tones (Tone 0) yield (A) longer peak latencies and (B) increased amplitude compared with late or on-time tones.

sis also displayed a two-way interaction between perturbation and tone position, $F(8,40) = 2.63$, $p < .05$ (Figure 4b). The focus of both interactions appears to be the response to early tones. At the locus of an early tone, the N100 had greater amplitude and occurred later relative to tone onset.

GAMMA-BAND ACTIVITY

We examined topographies of the evoked and induced GBA across a range of gamma frequencies (20–50 Hz). Figure 5 presents the data from two subjects (normalized power in the range 20–50 Hz) revealing the distribution of power across each subject's scalp within a 150-ms window centered at tone onset, for the on-time condition (no perturbation). Beneath the topographies, a time series is shown, averaging the response over all electrodes to illustrate the timing of peak power. Evoked responses (Panels A and B) consistently peaked after tone onset (time = 0 ms) with the main concentration of power observed in frontal electrodes. Induced activity (Panels C and D) varied more between subjects than evoked GBA in both latency and locus of peak power. For these two subjects, induced responses peaked before tone onset, with subsidiary peaks later (for other subjects, the main peaks in induced activity were observed at or just after tone onset, see below). The spatial distribution of power was overall more posterior than the evoked activity. This generally agrees with the topographical dissociation of the induced and evoked responses observed by Bertrand, Tallon-Beaudry, Giard, & Pernier (1998). However, the locus of induced GBA was highly variable between subjects. For this reason, no source analysis was conducted on these data.
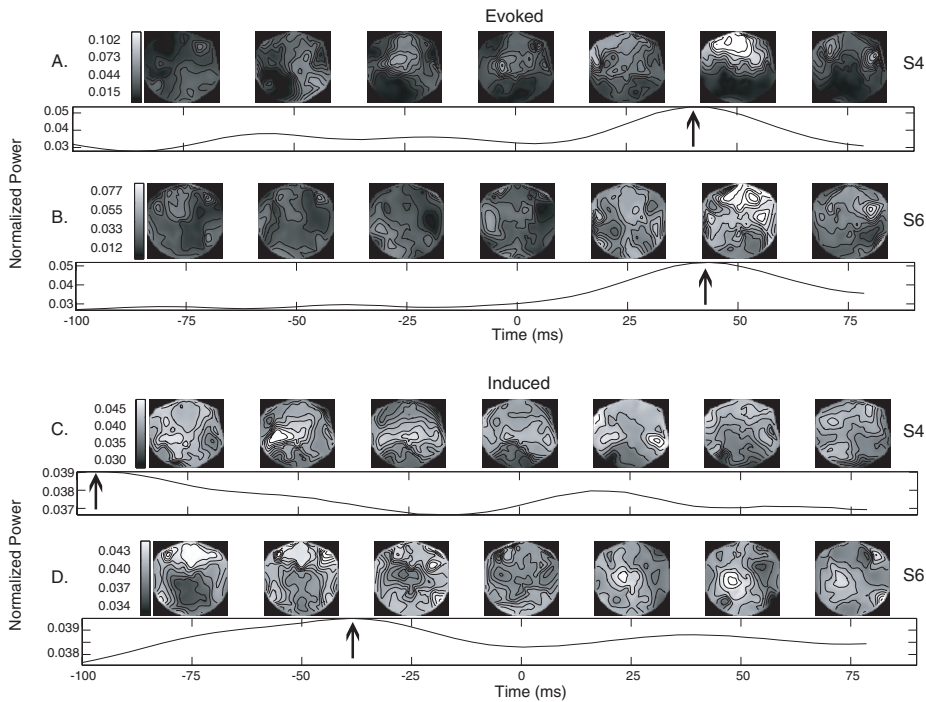
Fig. 5. Topographies of the evoked and induced gamma-band activity (GBA) for S4 and S6 accompanied by the time series averaged over all electrodes. The top portion of each topographical map represents the frontal electrodes, and the bottom represents occipital electrodes. (A, B) Evoked responses are distributed across frontal electrodes with peak latency after tone onset. (C, D) Induced responses are more widely distributed and variable across subjects. In general, induced power is more posterior and peaks earlier than evoked activity.

Instead, we concentrated on analyzing the latency of induced and evoked responses.

To analyze the latency of GBA without isolating individual sources, we calculated mean normalized power over all electrodes. This procedure facilitated the comparison between the timing of evoked and induced activity. Furthermore, this procedure decreased the signal-to-noise ratio slightly; however, as illustrated in Figure 5, the electrodes with the greatest peaks tended to dominate the average. We then computed summary time-frequency representations for each subject, illustrated in Figure 6. Peaks in both induced and evoked activity were time locked to the stimulus onsets. This was validated for the on-time condition by collapsing over frequency, and subjecting the resulting time series to a fast Fourier transform (FFT) (see Panels C and D). For every subject, evoked and induced activity displayed strong peaks at the stimulation rate of 2 Hz (500 ms).
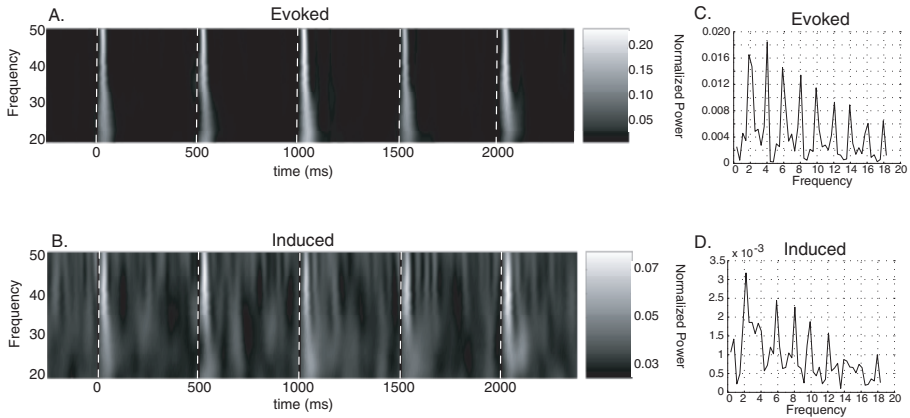
Fig. 6. Time-frequency (TF) representation and power spectra for S5 in the on-time condition. Dashed white lines represent tone onset. (A) Evoked activity is evident across all frequencies following tone onset. (B) Induced activity also peaks around tone onset across all frequencies. (C) Power spectra of the evoked response (20–50 Hz). Energy is mainly at 2 Hz (stimulation frequency) and 4 Hz (first harmonic), indicating the periodicity of the response. (D) Power spectra of the induced response (20–50 Hz). Most energy is concentrated at 2 Hz (stimulation frequency), also confirming the periodicity of gamma-band activity in relation to the stimulus.

Next, we identified peaks in induced and evoked TF representations (Figure 6), defined as the highest point in the TF plane within a time window around each tone onset.[1] Window size and position varied depending on the analysis (see below). This yielded a single peak corresponding to each tone onset, for a total of five GBA peaks (tone positions -1, 0, 1, 2, 3) for each type of GBA (evoked and induced) and each perturbation direction (early, on time, late), for each subject.

TIMING OF PEAK ACTIVITY

We next quantified the timing of induced and evoked GBA peaks. For the first analysis, we considered only the on-time conditions, and we defined a 300-ms window for peak detection centered at tone onset. We conducted a three-way ANOVA on the variables GBA type (induced, evoked), perturbation, and tone position, using peak latency (time of the peak relative to tone onset time) as our dependent measure. We found a single significant main effect of induced vs. evoked activity (repeated-measures ANOVA, $F(1,5) = 8.03$, $p < .05$ (see Figure 7). Induced peaks (*M*

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1. This technique does not guarantee that each peak is statistically significant. However, because it does not require reference to a prestimulus baseline (cf. Makeig, 1993), it allowed us to identify prestimulus activity. Moreover, because the peak is the highest point within the time window, it is a relatively conservative measure by which to evaluate potentially anticipatory activity.
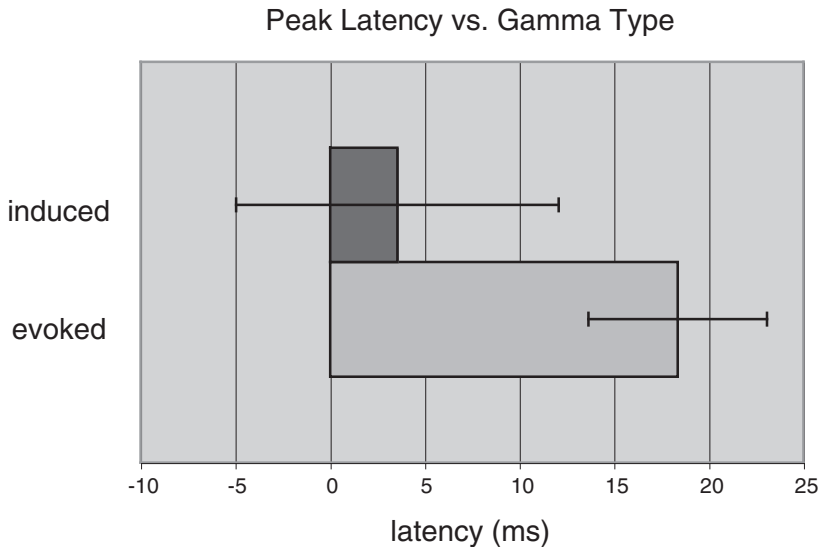
Peak Latency vs. Gamma Type

Fig. 7. Induced peak latency (top) is shorter than evoked peak latency and is not significantly different from tone onset (0 ms).

= 3.56 ms, *SD* = 80.73 ms) preceded evoked peaks (*M* = 18.36 ms, *SD* = 44.68 ms). The latency of the induced peak did not differ significantly from 0 ms.

Next, we measured the effect of perturbation direction on the latency of GBA peaks. For this analysis, we defined a 100-ms peak detection window centered at tone onset for the on-time condition. To capture peaks that occurred at expected times, we defined asymmetric windows for other trials (-50 ms to +175 ms for early trials, and −175 ms to +50 ms for late trials). We then conducted a three-way ANOVA on the variables GBA type, tone position, and perturbation direction, again using peak latency (time of the peak relative to tone onset time) as the dependent measure.

This analysis turned up a significant three-way interaction between GBA type, perturbation direction, and tone position, $F(8,40) = 2.22$, $p < .05$ (see Figure 8). Peaks in induced activity tended to precede tone onsets during late perturbation trials and to follow tone onsets during early perturbation trials. After both types of perturbations, the peaks slowly relaxed back toward synchrony with tone onsets. Peaks in evoked activity showed a different pattern, however. For on-time and late trials, evoked peaks occurred after tone onsets. But when tones occurred early, evoked responses were observed to have a much longer latency, and did not appear to relax toward baseline, at least not within the three tones after the perturbation.
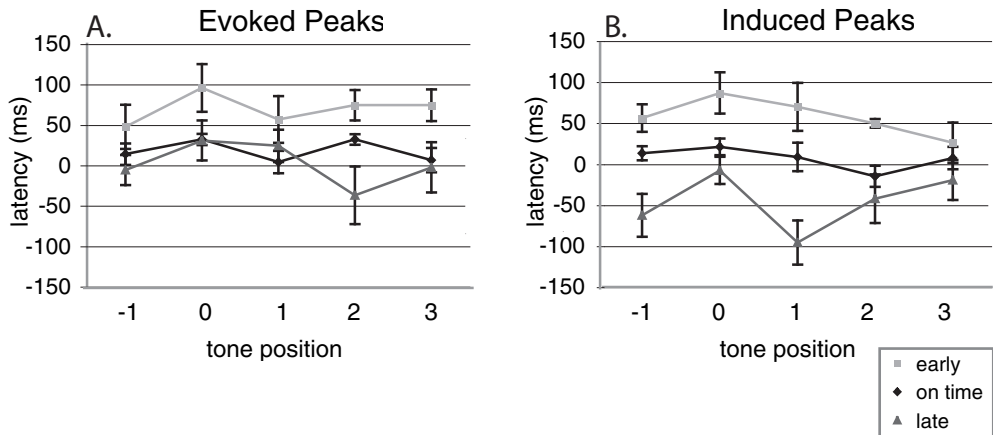
Fig. 8. Interaction of GBA type × perturbation direction × tone position. (A) Early tones produce later evoked peaks. (B) Early tones produce later induced peaks whereas late tones produce earlier induced peaks. Both yield relaxations back to baseline.

POWER OF PEAK ACTIVITY

Next, we quantified the peak normalized power of GBA. Using the same peak detection windows as in the previous analyses, we ran a second three-way ANOVA (GBA type × tone position × perturbation direction), this time using peak normalized power as the dependent measure. We observed a significant three-way interaction (GBA type × tone position × perturbation direction; $F(8,40) = 2.38$, $p < .05$). Peak evoked power was significantly higher at Tone 0 (the locus of the perturbation) when tones occurred early.

GRAND AVERAGE

The preceding results can be visualized quite nicely by averaging the TF representations over all subjects (Figure 9). This summary representation illustrates the commonalities among subjects and also points out some of the individual differences. Due to the nature of our normalization procedure, each subject's data contributes approximately equally to the average image. Thus the strongest peaks are seen where the responses of two or more subjects coincide, and in addition, individual subjects contribute many smaller peaks. For the on-time condition (middle panels), peaks are evident in both evoked and induced GBA, and both can be seen to be time-locked to the stimulus. Figure 9 also illustrates GBA for the early and late perturbation trials. Early tones produce a strong evoked peak following stimulus onset and an additional weaker evoked response (highlight-ed in the white box) at about the time the tone should have been expect-
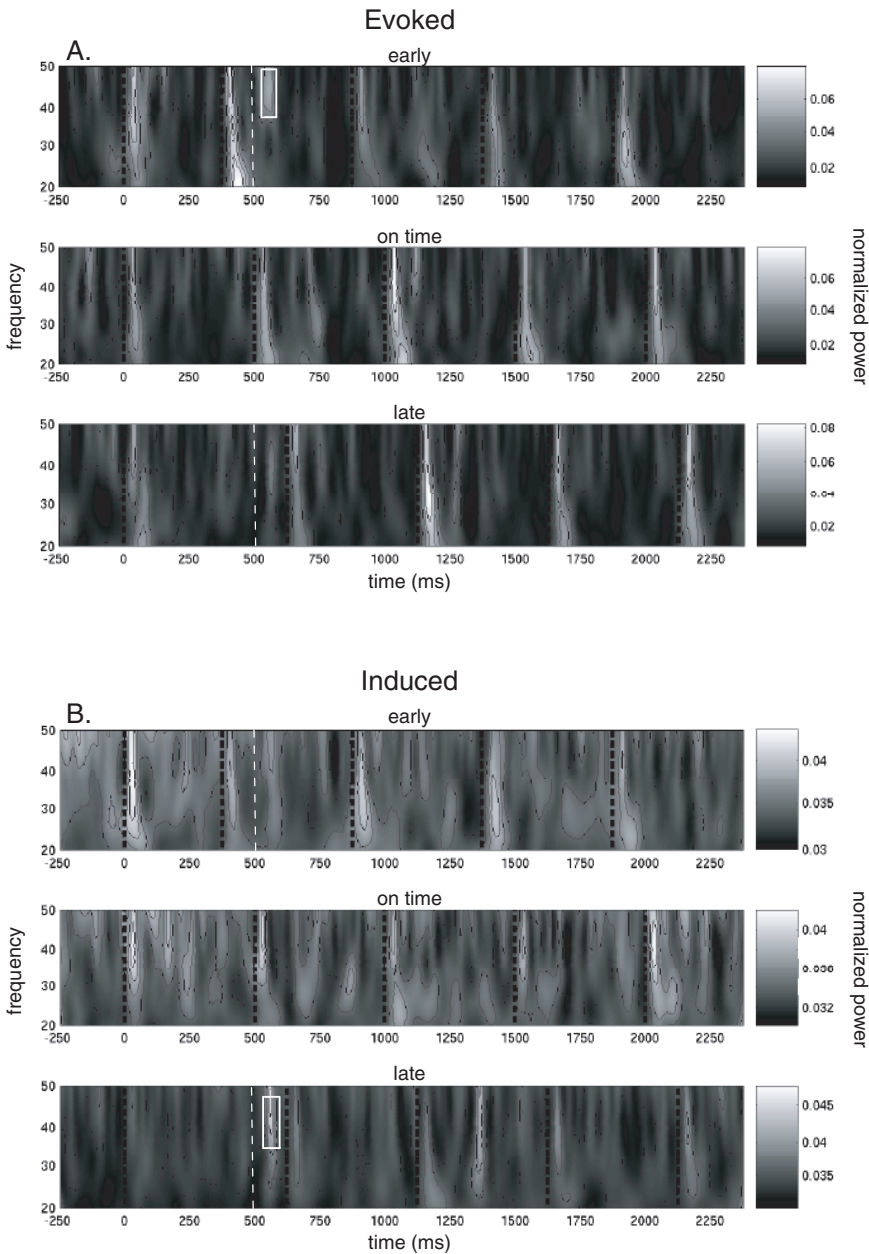
Fig. 9. Time-frequency (TF) representations averaged over all subjects and all electrodes. The black dashed lines denote tone onset; white dashed lines indicate where a tone was expected. The middle graphs from A and B show repetitive responses to the isochronous sequence. (A) Evoked response: Early tones produce an evoked peak 20 ms after stimulus onset and a smaller evoked response where the tone was expected (125 ms after the perturbed tone; response highlighted in a white box). (B) Induced response: 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.

ed to occur (dashed white line). Late tones yield an induced peak after stimulus onset, but an earlier peak (highlighted in a white box) appears to be a response to the absence of a tone where one was expected (dashed white line). It is also interesting to note the peak in induced activity subdividing the first and second tones following a late perturbation. This activity may represent some form of phase resetting.

Discussion

For isochronous sequences, induced GBA reached maximum power at about the same time as tone onsets on average. When onsets were late, peaks in induced GBA were observed at the times the tones should have been expected to occur and also in response to the late onsets. Overall, peaks in induced activity tended to precede tone onsets during late perturbation trials, and follow tone onsets during early perturbation trials, slowly relaxing toward synchrony after both types of perturbations. Evoked peaks were observed after tone onsets, at about 20-ms peak latency. When tones occurred early, however, evoked responses were observed to have a much longer latency and did not relax toward baseline, at least not within the three tones after the perturbation. Moreover, evoked peaks showed significantly greater power in response to early tones. By contrast, the latency of evoked responses was nearly identical for on-time and late trials. Overall, asymmetric GBA was observed in response to temporal perturbations.

We also observed a lag in peak latency and enhanced peak amplitude of the auditory N100 only at the locus of an early tone. This result could not be due merely to expectancy violation; it also represents an asymmetric response to temporal perturbations. This result contrasts with previous findings that the P50-N100 amplitude *decreases* with early tones (Prammstra, Turgeon, Hesse, Wing, & Perryer, 2003). However, Prammstra et al. used much smaller perturbations (50 ms) and measured the P50-N100 amplitude difference. Additionally, our N100 values were obtained by using a larger window (50–150 ms vs. 80–120 ms).

Our findings replicate a previous observation that peaks in induced GBA are, on average, synchronous with predictable tone onsets. Furthermore, the occurrence of induced peaks when expected tones were late, and the overall timing of induced peaks during perturbation trials, reinforce the general observation that induced GBA is anticipatory, and thus may represent a neural correlate of temporal expectancy for auditory sequences (Snyder & Large, in press). Our findings are also consistent with previous observations that auditory ERPs and evoked GBA represent responses to auditory stimulation (Carver et al., 2002; Pantev et al., 1991;

Snyder & Large, 2004, in press). Our peak latency for evoked GBA (~20 ms) was shorter than previously observed (Borgma, Ross, Draganova, & Pantev, 2001; Snyder & Large, 2004, in press); however, this may have been due to our perturbation methodology, to the structure of our stimuli, or to a combination of factors.

A particularly interesting observation is the apparent relaxation of the induced peaks after a temporal perturbation. This is similar to phase correction responses that have been observed in sensorimotor synchronization tasks that use a temporal perturbation methodology (Large et al., 2002; Repp, 2002a) as well as to responses that are predicted by models of entrainment and phase correction (Kelso, DelColle, & Schöner, 1990; Large & Jones, 1999; Vorberg & Wing, 1996). This could explain recent observations suggesting a synchronization of perceptual processes underlies synchronization of motor activity (Repp, 2002b). One apparent difference is that relaxation of induced GBA, measured as number of events, is slower than the relaxation responses observed in sensorimotor synchronization (Large et al., 2002). One possibility is that our participants were not required to perform any overt perceptual or motor task, they were merely instructed to listen attentively, thus they had no incentive to respond quickly to timing changes.

It is also interesting to observe that gamma-band responses to phase perturbations were asymmetric. Induced peaks were observed at expected onset times when tones were late, but not when tones were early. Evoked peaks were observed at expected onset times when tones were early, but not when tones were late. Furthermore, early tones produced an increase in evoked GBA power. Thus, early tones seem to come as a surprise, whereas late tones are actively missed. Most models of entrainment and phase correction assume temporally symmetric responses to phase perturbations; however, our observations, coupled with recent observations regarding temporal perturbations in both perceptual and motor tasks (Large & Jones, 1999; Repp, 2002a) suggest that responses to larger temporal perturbations are not symmetric. Mackenzie and Jones (2004) used a delayed comparison task in which participants judged pitch differences between a comparison and a standard tone embedded within a rhythmic sequence. They demonstrated an asymmetry such that listeners perform pitch comparisons most poorly if the comparison tone is presented earlier than expected. In addition, the error related negativity, an ERP component associated with performance monitoring, has been reported to occur only in response to perceptibly late tones (Praamstra et al., 2003).

Gamma-band activity appears to be a useful neuroelectric correlate of anticipation and expectation. The fact that anticipatory activity is observed in the gamma band suggests a relationship to attentional processing, although this relation remains speculative. Future work must

manipulate the attentional state of subjects, investigate the relationship of gamma-band processes to performance of perceptual and motor tasks, and attempt to localize the neural source of anticipatory activity. As to whether or not pulse is primarily a motor response (Todd et al., 1999) or it is attentional in nature (Large & Jones, 1999), these observations begin to address the questions, but do not fully answer them. It may be that gamma-band processes underlie both perceptual and motor responses and act to coordinate spatially distinct cortical activities.[2]

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