

Stimulus-dependent oscillations and evoked potentials in chinchilla auditory cortex

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Abstract Besides the intensity and frequency of an auditory stimulus, the length of time that precedes the stimulation is an important factor that determines the magnitude of early evoked neural responses in the auditory cortex. Here we used chinchillas to demonstrate that the length of the silent period before the presentation of an auditory stimulus is a critical factor that modifies late oscillatory responses in the auditory cortex. We used tetrodes to record local-field potential (LFP) signals from the left auditory cortex of ten animals while they were stimulated with clicks, tones or noise bursts delivered at different rates and intensity levels. We found that the incidence of oscillatory activity in the auditory cortex of anesthetized chinchillas is dependent on the period of silence before stimulation and on the intensity of the auditory stimulus. In 62.5% of the recordings sites we found stimulus-related oscillations at around 8–20 Hz. Stimulus-induced oscillations were largest and consistent when stimuli were preceded by 5 s of silence and they were absent when preceded by less than 500 ms of silence. These results demonstrate that the period of silence preceding the

stimulus presentation and the stimulus intensity are critical factors for the presence of these oscillations.

Keywords Auditory cortex · Chinchilla · Oscillations · Local field potential · Tetrode

Abbreviations

EP Evoked potential
LFP Local field potential

Introduction

Neural oscillations have been found in different areas of the mammalian brain (for a review see Buzsáki and Draguhn 2004). They were discovered in the olfactory system and have been correlated with stimulus presentation (Adrian 1950). Fast electrical non-stimulus-locked (induced) oscillations have been found in visual cortex of anesthetized and awake cats (Gray and Singer 1989; Eckhorn et al. 1988; Gray and Viana di Prisco 1997). These oscillations have also been observed in the visual cortex of awake monkeys (Friedman-Hill et al. 2000) and they have been proposed to participate in a mechanism involved in binding different features of a visual scheme (Gray 1999).

Stimulus-related oscillations reported in the auditory cortex could be divided in two groups: (1) high frequency induced-oscillations (>30 Hz) and (2) stimulus locked and unlocked low-frequency oscillations (<20 Hz). Stimulus-related high frequency oscillations have been found in local field potential (LFP) recordings from auditory cortex of halothane anesthetized rats (Franowicz and Barth 1995; Barth and MacDonald 1996) and ketamine anesthetized monkeys (Brosch et al. 2002). Spontaneous low-frequency oscillations (around 10 Hz) have been found in unit recordings

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from the auditory cortex of anesthetized rats (Maldonado and Gerstein 1996), and from the medial geniculate body of cats (Galambos et al. 1952). While, stimulus locked and non-locked oscillations have been reported in unit recordings from auditory cortex of anesthetized rats (Cotillon et al. 2000; Cotillon and Edeline 2000) and cats (Eggermont 1992; Eggermont and Smith 1995; Dinse et al. 1997; for a review of oscillations in the auditory system see Cotillon-Williams and Edeline 2004). The functional implications of these low-frequency oscillations are still unclear.

Many of these oscillations are proposed to be of internal origin (Fries et al. 2007), thus they are dependent not only on the stimulus, but also on the ongoing state of the neuronal network. We hypothesized that the auditory cortex has different cortical states during auditory stimulation and during resting (silent) periods and that these states may modulate the incidence and strength of the oscillatory activity in the auditory cortex. The aim of this study was to examine and characterize the stimulus-related oscillatory activity of auditory responses in the LFP signals recorded from the auditory cortex of anesthetized chinchillas (*Chinchilla laniger*; Spotorno et al. 2004). We investigated their properties and relationship with stimulus intensity, frequency, and inter-stimulus interval.

Methods

Animals and surgical procedures

Surgical and experimental techniques were performed in accordance with institutional guidelines. Ten adult male chinchillas (400–700 g) served as subjects for this study. The chinchillas were anesthetized with ketamine (20 mg/kg im) and acepromazine (0.7 mg/kg im). The anesthetic protocol included atropine sulfate (0.04 mg/kg im). Supplemental doses of ketamine (10 mg/kg) were given at approximately 30–45 min intervals, depending on the anesthetic level judged by the foot withdrawal reflex. Body temperature was maintained at 37°C. The head was stabilized with a fixation device that allowed free access to the external meatus. A tetrode was positioned in the left auditory cortex following descriptions given by Harrison and coworkers (Harrison et al. 1996; Harel et al. 2000). The dura mater was incised, the penetration site was covered with agar and a tetrode was lowered into the cortex (700–1,100 μm depth), through the incision, with a hydraulic microdrive (David Kopf Instruments Model 1207B). A screw anchored to the skull served as a reference.

Acoustic stimuli and electrophysiology

All experiments were performed in a double-walled sound attenuating room. Auditory stimuli were digitally generated

(100 kHz) with a Real-Time Processor (RP2.1) from Tucker-Davis-Technologies system III (TDT III), and attenuated in steps of 2–20 dB with a programmable attenuator (PA5 from TDT III). Auditory stimuli were delivered with an electrostatic driver (ED1 from TDT III) that powers an electrostatic speaker (EC1 from TDT III) that was connected with a sealed tube into the right external auditory meatus. Tone and noise bursts had a 5 ms ramp and a total duration of 15 ms. We used two types of noise bursts: (1) white noise and (2) three different band-passed noises (1–2 kHz; 2–4 kHz; and 4–8 kHz). Clicks were square pulses of 100 μs wide. Auditory stimuli were delivered at presentation rates from 1 up to 20 Hz and levels ranging from 0 to 108 dB SPL. Each trial consisted of a 4 s stimulus presentation and simultaneous signal recording, followed by a 5 s inter-trial time (total trial time 9 s). For each condition 30–40 trials were stored and analyzed off-line by an interactive custom-made computer program.

Local field potentials (LFP) signals were obtained with a custom-fabricated nichrome tetrode whose impedance was adjusted to 1 M Ω measured at 1 kHz. For a complete description on tetrode construction see Gray et al. (1995). The signals were amplified (10 K), band-pass filtered (1–300 Hz) and digitized (20 kHz/channel) with a custom-made program using a National Instrument board housed in a Pentium IV PC.

Data analysis

We divided the signal from the tetrodes into two bands; the high frequency band was used to isolate unit activity (not reported in this paper) and the low frequency band (1–300 Hz) to study the LFP signal. Off-line data analyses were carried out with a custom-made software programmed in C Language (LabWindows[®] 5.0 by National Instruments). Evoked potential (EP) amplitudes were calculated from the peak-to-peak signal in microvolts. The occurrence in time of stimulus-induced oscillations has large variability. For that reason, the magnitude and preferred frequency of the oscillation were measured in each trial, and the averages of single-trials spectra were calculated. We used the power spectrum of the fast-Fourier transform with a 205 ms window at 4.9 Hz resolution, or a 102 ms window at 10 Hz resolution. To avoid the large amplitude frequency components of the EP, the first 50 ms of each trial were excluded from the Fourier analysis.

Results

A total of 192 tetrode recordings from 16 different primary auditory-cortex sites that exhibited clear auditory evoked responses with short latencies were analyzed from the ten chinchillas. Tetrode recordings were identified as belonging

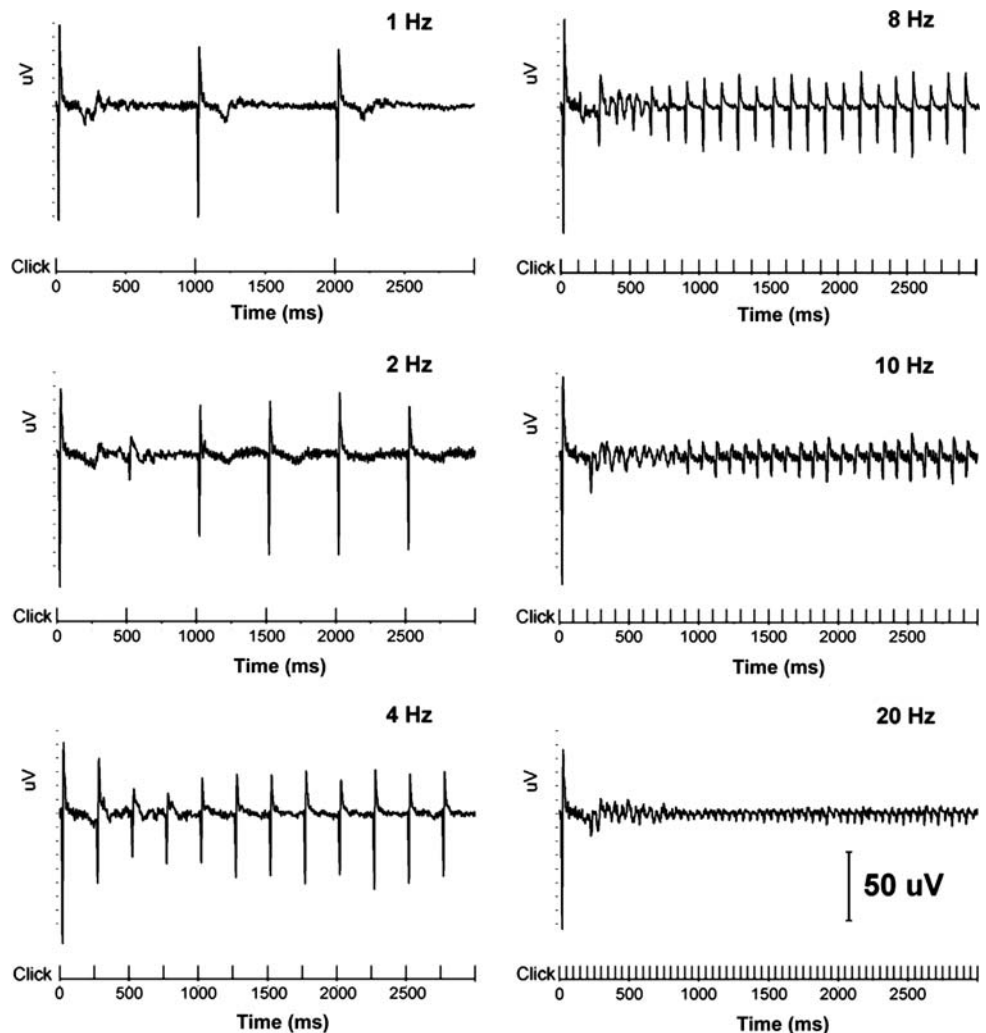
to the primary auditory cortex based on two criteria: electrode position referred to blood vessels (Harrison et al. 1996) and short onset-response latencies (<15 ms, Harel et al. 2000). Figure 1 shows averaged evoked responses from the auditory cortex in one chinchilla to trains of clicks presented at different rates (1–20 Hz). The first EP of each graph, which is preceded by 5 s of silence, has the largest amplitude compared to subsequent EPs. However, the EPs did not decrease steadily. Examination of Fig. 1 (particularly for rates at 2, 4, and 8 Hz) shows that the EPs evoked between about 350 and 650 ms typically had lower amplitudes than those evoked later on each trial.

An apparent reason for these non-uniformities is the occurrence of oscillations in the LFP signals that follow the EP (as seen in Fig. 1), particularly, after the first EP of the trial. Figure 2 shows raw data obtained with a 1 Hz click-train, in which induced oscillations (8–20 Hz) could be clearly seen in single trials. However, there was trial-to-trial variability in their presence, latency, duration, and magnitude (Fig. 2a). Figure 2b shows the corresponding power spectra

of the Fourier transform of each trial. The stimulus-induced oscillations were stronger and longer for the first stimulus of the train than for successive clicks, tones or noise bursts.

Figure 3a shows an example of EPs in two different recording sites. In the first recording site there was stimulus-induced oscillatory activity, while in the second site there was none. In the recording of the first site, the EP amplitude diminished in the presence of the oscillations (see the EP in the 500-ms epoch). In contrast, in the second-site recording there was no oscillatory activity and only a small reduction in EP amplitude during the click train. Figure 3b displays for all click rates, the mean amplitude calculated for EPs evoked 1,000 ms after the beginning of the trials normalized by the mean amplitude of the EP evoked after 5,000 ms of silence (points at 0.2 Hz rate). As the stimulus click rate was increased, there was a decrease in EP amplitudes, which was consistent for all click rates. The figure also shows the mean amplitude of induced oscillations for all click rates normalized by the amplitude of the oscillations induced by a click rate of 0.2 Hz (after

Fig. 1 Local field potentials recorded from the auditory cortex of the chinchilla. Each trace represents an average of click-evoked responses from 30 trials. The first evoked potential of each trial is preceded by 5 s of silence. The click-rate is shown in the upper-right position and the time of presentation of each click is indicated by a vertical trace in the abscissa of each graph. For higher click rates the evoked potentials have lower amplitudes. For 2, 4, and 8 Hz it is possible to see that the potentials evoked between 350 and 650 ms had lower amplitudes than those evoked later on each trial, more than 1,000 ms after the beginning of each trial



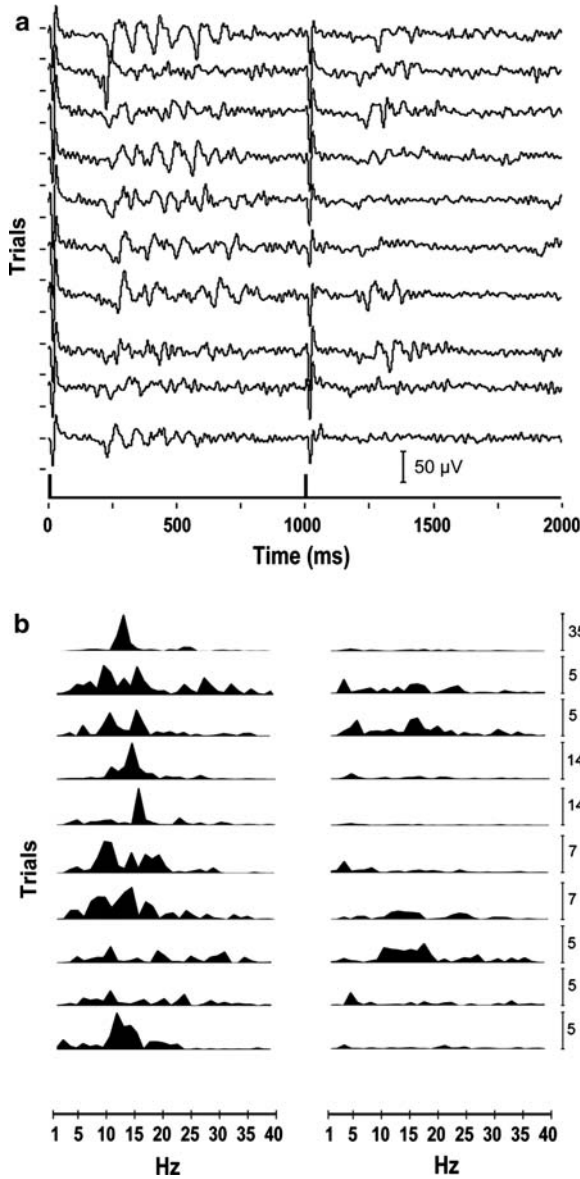


Fig. 2 Stimulus-dependent oscillations in single trials. **a** Local field potentials from ten sequential single trials obtained with a click-train of 1 Hz. The oscillations induced by the first stimulus of each trial that is preceded by 5 s of silence are the biggest and decrease in amplitude for later stimuli. **b** Power spectra of the corresponding single trials shown on the top panel. Spectra at the left column were computed from 50 to 869 ms (time window of 819 ms, resolution of 1.2 Hz). Spectra at the right column were calculated between 1,050 and 1,869 ms (time window of 819 ms, resolution of 1.2 Hz). The scale for each trace is shown on the corresponding right abscissa

5,000 ms of silence). The mean amplitude of the induced oscillations was largest for a click rate of 0.2 Hz, decrease monotonically at higher rates and oscillations were absent for rates higher than 2 Hz.

To characterize these auditory induced oscillations, we performed a trial-to-trial Fourier analysis and calculated the average power spectrum for each stimulus condition. We

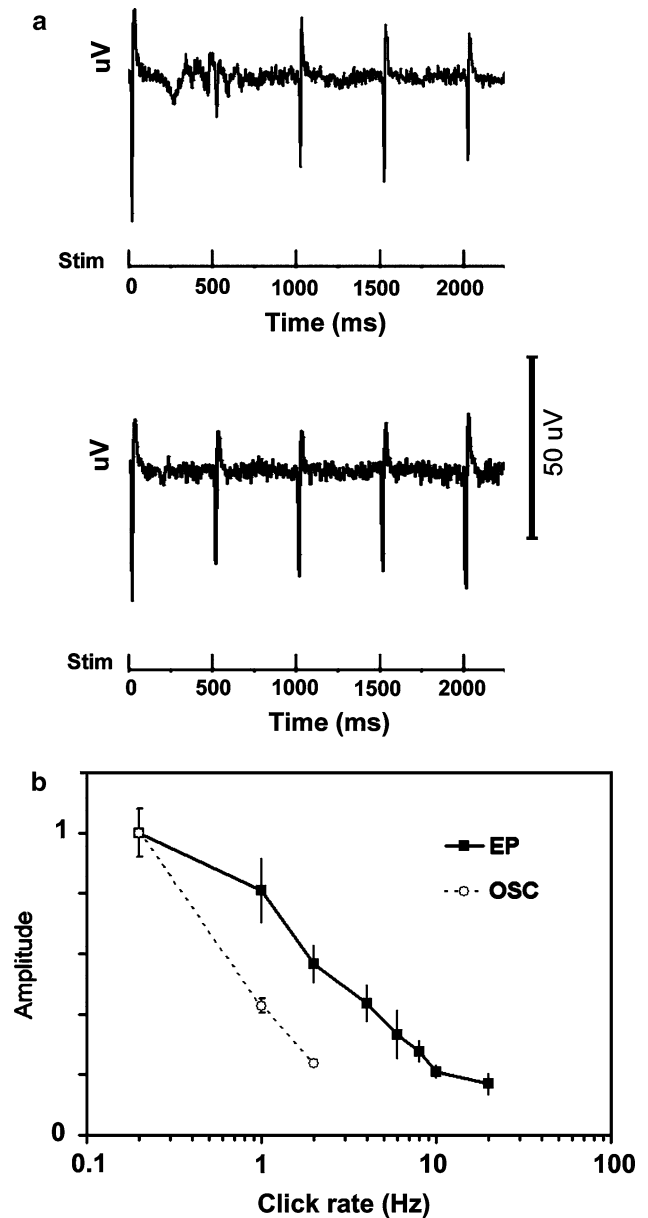


Fig. 3 Amplitudes of auditory evoked potentials at different click rates with and without oscillations. **a** Each trace represents an average of 2 Hz click-evoked responses from 30 trials, the upper trace shows EPs in the presence of oscillations while the lower trace shows EPs without oscillations. **b** Amplitude of cortical evoked potentials and induced oscillations normalized to the amplitude at the lowest rate (0.2 Hz), plotted against stimulus rate. Measurements of EPs were made from potentials evoked later than 1,000 ms after the beginning of each trial. Points at 0.2 Hz correspond to the amplitudes of EPs and induced oscillations in response to auditory stimuli preceded by 5 s of silence

evaluated the significance of these oscillations in each single trial using the following criteria: (1) a minimum threshold for oscillation magnitude of 3 µV, which was typically twice the baseline signal noise and (2) a magnitude of the power-spectrum peak that exceeds the mean plus three standard deviations of the power-spectrum

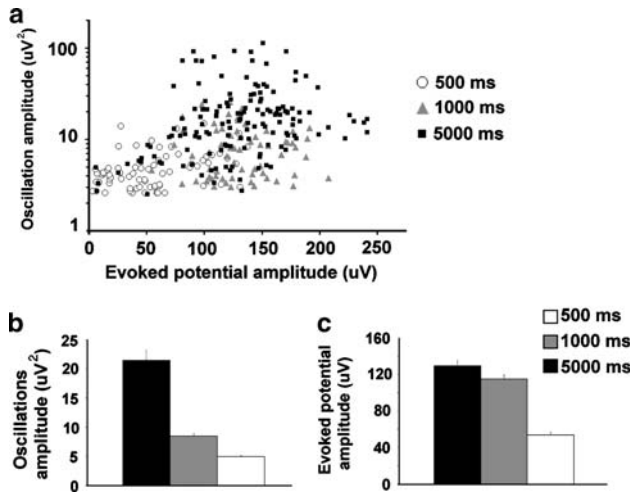


Fig. 4 Relationship between EP and induced-oscillations amplitudes. **a** Mean power of oscillations plotted against amplitude of averaged evoked potentials in all recordings with 0.5, 1.0, and 5.0 s of silence that had oscillations. Note that most oscillations that have a power $>10 \mu\text{V}^2$ were induced by stimuli preceded by 5 s of silence. **b** Average oscillations amplitude. **c** Average EP amplitude with 0.5, 1.0, and 5.0 s of silence

values ($P < 0.01$). Applying these criteria we found low-frequency induced oscillations (8–20 Hz) in the signals recorded from seven of the ten chinchillas and in ten of the sixteen recording sites.

Figure 4a depicts the relation between the average amplitude of the EPs preceded by 500 ms, 1 s, and 5 s of silence and the magnitude of the induced oscillations. The induced oscillations preceded by 5 s of silence reached higher magnitudes than those preceded by 1 s and 500 ms. The mean average power of the oscillations displayed a non-linear relation with the amplitude of the EPs. Figure 4b, c display the mean amplitude of the induced oscillations and of EPs preceded by 500 ms, 1 s, and 5 s of silence, which show that the larger the time between stimulus presentations, the stronger the subsequent induced oscillations.

We found that stimulus intensity is also a critical factor for the presence of oscillations; only moderate (>50 dB SPL) to high intensity stimuli induced these late oscillations in the auditory cortex (Fig. 5a). Because clicks are distinctive in that they contain power in a wide range of frequencies, we compared the appearance of oscillations induced by tones of different frequencies (1, 2, 3, 4, 6, and 8 kHz) and clicks at different intensities. We also studied oscillatory activity evoked by white noise and three band-pass noises (1–2 kHz; 2–4 kHz; and 4–8 kHz) at different sound-pressure levels. Oscillations did not appear to be tuned to any of the stimulus frequencies and no frequency dependencies or selectivity were found, as assessed by tones, clicks, white noise, or the different types of band-pass noise (Fig. 5b).

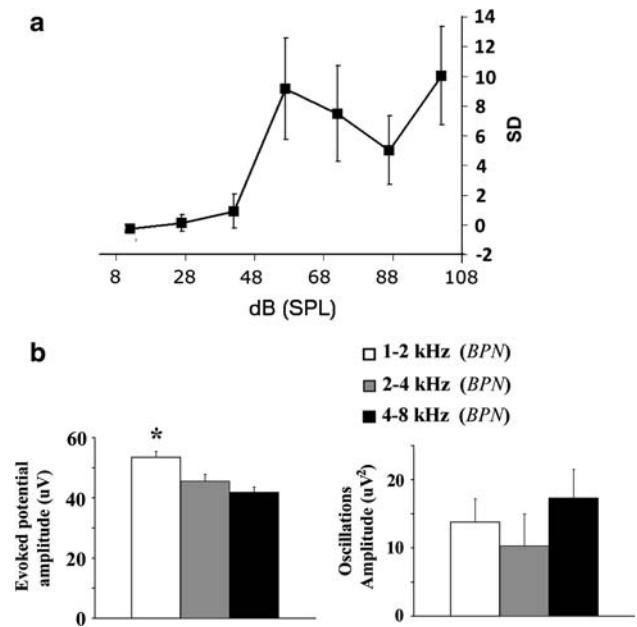


Fig. 5 Intensity dependence and frequency independence of auditory induced-oscillations. **a** Grand average intensity function of auditory oscillations measured in standard deviations. Note that significant auditory oscillations (3 SD above mean amplitude) appear only for stimuli louder than 50 dB SPL. **b** *Left panel*: average amplitude of auditory evoked potentials in response to three different band-pass noises (BPNs: 1–2 kHz; 2–4 kHz; 4–8 kHz). The magnitude of the average potential evoked by the 1–2 kHz noise was significantly larger than the mean potentials evoked by the 2–4 and 4–8 kHz noises at the same sound-pressure level (*ANOVA, Tukey test; $F = 8.73$; $P < 0.001$). *Right panel*: average amplitudes of induced oscillations using the same three band-pass noises. No significant amplitude differences were found

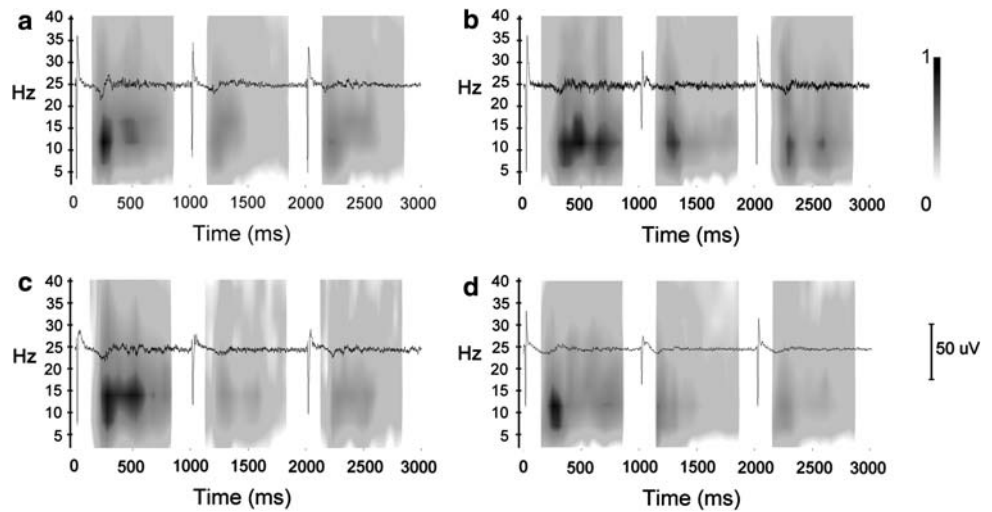
To examine the dynamics of these oscillations in time, we computed a windowed FFT analysis of the responses to click trains. The oscillations exhibited a latency of 200–300 ms, regardless of click frequency, and the rhythmic activity could last for more than 500 ms. In Fig. 6 we show an example of this analysis for click trains of 1 Hz rate in recording sites, that belong to four different chinchillas, with the corresponding averaged EPs. Oscillations appeared 200–300 ms after the first EP and they diminished after EPs evoked by the second and third click stimuli.

Discussion

Characterization of auditory cortex oscillations

We demonstrate that induced oscillatory activity in the auditory cortex is present only for auditory stimuli louder than 50 dB SPL, preceded by silent periods longer than 500 ms. However, oscillations may be present at stimulus intensities below 50 dB SPL, but they could be not detectable given the poor signal to noise ratio. Typically when

Fig. 6 Examples of averaged time spectrograms and superimposed averaged evoked potentials in four different chinchillas. Click trains were presented at 1 Hz. Each time window had duration of 205 ms and successive time windows were overlapped by 50 ms. In all cases the first 50 ms after each evoked potential were excluded from the Fourier analysis. The gray scale was normalized to maximum power amplitude and bins were digitally interpolated



neurons of the auditory cortex are stimulated at increasing rates, early responses can be entrained by the stimulus up to a given rate, above which neural responses cannot synchronously follow the stimulus, and the spike-stimulus transfer function resembles a low-pass filter (Fig. 3b; Langner 1992; Joris et al. 2004). A reduction in magnitude of auditory-cortex responses to increasing stimulus rates has been previously reported in rats (Kilgard and Merzenich 1998), cats (Phillips et al. 1989; Eggermont 1991, 1992) and monkeys (Lu et al. 2001). The relation between auditory cortex EP amplitude and stimulus rate in the awake chinchilla has been examined by Burkard et al. (1999). They showed a progressive reduction in amplitude of cortical EPs with increasing noiseburst rates, which is in agreement with our results. However, they did not study rates below 10 Hz, and according to our data the normalized amplitude of the EP at 10 Hz rate is about 20% of that evoked with 5 s of previous silence (see Fig. 3b). Besides, they did not report amplitude differences between the first and subsequent cortical EPs in each trial, as shown in our data.

We found significant oscillations in the LFP signal with peaks around 10 Hz, which were stronger for click presented at low frequencies. Burkard and colleagues did not report oscillations in the auditory cortex of the awake chinchilla, but based upon our data there are no induced oscillations for stimuli presented at 10 Hz rate. However, probably another reason that could explain the presence of oscillations in our recordings and the apparent lack of oscillations in their work is that our recordings were performed in anesthetized and theirs in awake chinchillas. Cotillon and collaborators examined the incidence of oscillations in the auditory cortex of awake rats (Cotillon-Williams and Edeline 2003). They only found stimulus-locked oscillations in anaesthetized animals and in the slow-wave sleep condition, but not in the wake or paradoxical sleep condition. Another study performed in awake bats did not find

unit oscillations, either in peristimulus histograms or in autocorrelograms (Horikawa et al. 1994). Further research with an adequate experimental design may be needed to find the condition under which these oscillations occur in awake animals.

The oscillations that we have observed exhibited peaks at about 10 Hz and were largest 200–300 ms after stimulus onset. The frequencies of these oscillations (8–20 Hz) are similar to those described in unit recordings by Eggermont (1992) and by Cotillon et al. (2000) and in LFP recordings by Eggermont and Smith (1995). Our results show that periods without auditory stimuli appear to be an important factor in the incidence and strength of these oscillations. In our study they were apparent only when the silent period before stimulation was longer than 500 ms. Similarly, stimulus-related oscillations in the auditory cortex have been found for silent periods before stimulation longer than 1,000 ms in rats (Cotillon et al. 2000; Cotillon and Edeline 2000) and 125 ms in cats (Eggermont 1992). Although we observed that the oscillations in the LFP signal were not dependent on stimulus frequency, they were more reliable and bigger for click stimuli than for tones or noise bursts, which is also in agreement with oscillations reported in rat auditory-cortex units by Cotillon et al. (2000).

Origin of auditory oscillations

Cotillon et al. (2000) found low-frequency oscillations in the medial geniculate body and the auditory sector of the reticular nucleus. When the auditory reticular nucleus was inactivated, spontaneous low-frequency oscillations were abolished in the auditory cortex. Inactivation of the auditory cortex, however, did not affect low-frequency oscillations in the auditory reticular nucleus. Consequently, they concluded that low-frequency oscillations in the auditory system are generated from the interaction between the

thalamus and the reticular nucleus. The thalamic origin of low-frequency oscillations is also supported by simultaneous intracellular recordings from the motor cortex and the ventrolateral nucleus of the thalamus, which showed that thalamic bursts appeared always before cortical oscillations (Grenier et al. 1998).

Besides a feasible thalamic origin of these low-frequency oscillations, it is possible that a cortical mechanism is also involved in this phenomenon. Kenmochi and Eggermont (1997) have shown that the dominant frequency of the spontaneous local-field oscillation in the auditory cortex of ketamine anesthetized cats is correlated with the single unit's best modulation frequency in response to click trains of different rates.

Two states in the auditory cortex: silence and auditory stimulation

In a recent work Tomita and Eggermont (2005) have shown that correlation between spikes of auditory-cortex neurons is higher during long periods of silence than during periods of auditory stimulation outside their spectro-temporal receptive fields. They suggested that stimulation breaks up large assemblies of neurons that appear during long periods of silence. This finding is in agreement with our results, as we found that late oscillations occur with intense auditory stimuli after a silent period. Probably the silent period allows the generation of neuronal assemblies, which in response to a sudden stimulus generate these late oscillations.

In nature an auditory stimulus that suddenly breaks a quiet environment could help a subject to survive from a possible danger by increasing the arousal and attentional level. We propose that the first auditory stimulus after a long silent period delimits a change between two different cortical states: from a resting state during the silent period to another of auditory stimulation, and that the oscillatory neural activity reflects the change between these cortical states. The changes in EP magnitude and oscillatory activity could also be explained by sensory adaptation. Probably the amplitude reduction of EPs produced after the oscillations epoch ($>1,000$ ms; see Fig. 1) is directly related to adaptation. However, the greater reduction of EPs evoked between 350 and 650 ms (see Fig. 1, at 2, 4, and 8 Hz) is probably produced by the presence of oscillations and is more related to the change between silent and stimulation periods, than to sensory adaptation.

LFP oscillations have been found in almost all animals and in different brain structures; however, the role of low-frequency oscillations in the auditory system is still unclear (Cotillon-Williams and Edeline 2003). It has been postulated that oscillations are a mechanism that enables the enhancement of communication among groups of neurons. Fries

(2005) hypothesized that this may be mechanistically subserved by neuronal coherence. Activated neuronal groups oscillate and thereby undergo rhythmic excitability fluctuations that produce temporal windows for communication. We postulate that the neuronal dynamics of the auditory cortex, which has not been stimulated for a long period of time, appears to be modulated by its ongoing activity such that it favors an oscillatory response to a sudden stimulus.

One implication of the increased oscillations observed in the first response after a silent period relates to the possibility that these oscillations help to ensure an increase in neuronal synchronization, enhancing communication, and processing among neurons (Fries et al. 2007).

One possible mechanism that originates these oscillations involves cortical neurons with strong reciprocal synaptic connections that oscillate on subthreshold potentials. This has the effect of synchronizing onset latencies of auditory responses across these neurons (Fries et al. 2001). Beta (8–20 Hz) and gamma (>30 Hz) oscillations are sustained by synchronous oscillatory activity of inhibitory interneurons that induces periodic inhibition of pyramidal cells (for review see Whittington et al. 2001). It has been shown that inhibitory phasing is particularly effective in synchronizing the discharges at the onset of responses (Erchova et al. 2004) but may be overridden once the excitatory drive exceeds a certain level. This could explain why the first stimulus evokes the strongest oscillation, but successive stimuli lack effectiveness to elicit these oscillations.

In conclusion: we demonstrated that the period of silence before the stimulus presentation and the intensity level are critical for the presence of these low-frequency oscillations, and we suggest that these oscillations originate during the transition between two different cortical states.

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