Beta oscillatory power modulation reflects the predictability of pitch change

Andrew Chang[a], Dan J. Bosnyak[a, b], Laurel J. Trainor[a, b, c]

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[a]Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON, Canada
[b]McMaster Institute for Music and the Mind, McMaster University, Hamilton, ON, Canada
[c]Rotman Research Institute, Baycrest Hospital, Toronto, ON, Canada

Corresponding author: Laurel J. Trainor (ljt@mcmaster.ca), Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON, L8S 4K1, Canada.

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Abstract

Humans process highly dynamic auditory information in real time, and regularities in stimuli such as speech and music can aid such processing by allowing sensory predictions for upcoming events. Auditory sequences contain information about both the identity of sounds (what) and their timing (when they occur). Temporal prediction in isochronous sequences is reflected in neural oscillatory power modulation in the beta band (~20 Hz). Specifically, power decreases (desynchronization) after tone onset and then increases (resynchronization) to reach a maximum around the expected time of the next tone. The current study investigates whether the predictability of the pitch of a tone (what) is also reflected in beta power modulation. We presented two isochronous auditory oddball sequences, each with 20% of tones at a deviant pitch. In one sequence the deviant tones occurred regularly every fifth tone (predictably), but in the other sequence they occurred pseudorandomly (unpredictably). We recorded the electroencephalogram (EEG) while participants listened passively to these sequences. The results showed that auditory beta power desynchronization was larger prior to a predictable than an unpredictable pitch change. A single-trial correlation analysis using linear mixed-effect (LME) models further showed that the deeper the pre-deviant beta desynchronization depth, the smaller the event-related P3a amplitude following the deviant, and this effect only occurred when the pitch change was predictable. Given that P3a is associated with attentional response to prediction error, larger beta desynchronization depth indicates better prediction of an upcoming deviant pitch. Thus, these findings suggest that beta oscillations reflect predictions for *what* in additional to *when* during dynamic auditory information processing.

Keywords: Sensory prediction; Predictive coding; Beta oscillation; P3a; Electroencephalogram (EEG); Auditory cortex

1 Introduction

Humans need to process highly dynamic, fleeting incoming sensory information in real time, including speech and music. Structural regularities (e.g., beat, meter and pitch patterns in music; timing, stress, phonological, syntactic and semantic structure in speech) and the context in which sensory events occur allow predictability, which can greatly simplify the problem. Indeed, there is considerable evidence that sensory systems extract regularities from perceived external events and predictively encode upcoming sensory input, including *what* (predictive coding) it might be and *when* (predictive timing) it might happen (Arnal & Giraud, 2012; Friston, 2005; Heilbron & Chait, 2017; Nobre, Correa, & Coull, 2007; Schröger, Marzecová, & SanMiguel, 2015; Winkler, Denham, & Nelken, 2009), which facilitates perceptual processing in real time (Henry & Obleser, 2012; Henry, Herrmann, & Obleser, 2014; Hickok, Farahbod, & Saberi, 2015; Rohenkohl, Cravo, Wyart, & Nobre, 2012). Prediction is also essential for anticipatorily deploying auditory attention (Large & Jones, 1999; Schroeder & Lakatos, 2009) and coordinating motor actions (Chang, Livingstone, Bosnyak, & Trainor, 2017; Kragness & Trainor, 2016, 2018; Trainor, Chang, Cairney, & Li, 2018; Warren, Wise, & Warren, 2005).

Neural oscillatory activities are regarded as essential neural mechanisms for sensory prediction. The power of beta band (~20 Hz) has been shown to reflect predictive timing (Arnal & Giraud, 2012; Cirelli et al., 2014; Fujioka, Ross, & Trainor, 2015; Fujioka, Trainor, Large, & Ross, 2012; Morillon & Baillet, 2017), but whether it reflects predictive coding (the *what* domain) remains unclear. Previous electroencephalographic (EEG) and magnetoencephalographic (MEG) studies show that when listening to an isochronous tone sequence, induced (non-phase-locked) beta oscillation in bilateral primary auditory cortices desynchronizes following the onset of each tone, resulting in a power decrease, and then resynchronizes prior to the onset of the upcoming tone. This power fluctuation is proposed to reflect temporal entrainment and temporal prediction because the slope of the resynchronization depends on the presentation speed of the isochronous tones (Cirelli et al., 2014; Fujioka et al., 2012), and because beta power modulation is disrupted in non-rhythmic sequences or by occasionally omitted tones (Fujioka et al., 2012, 2009; Snyder & Large, 2005). Outside of a rhythmic context, beta power has also been shown to reflect the predictability of a temporal gap between tone pairs (Todorovic, Schoffelen, Van Ede, Maris, & De Lange, 2015). Furthermore, beyond the traditional view that beta oscillation reflects cortical communication between sensory (especially, auditory) and motor regions (Fujioka et al., 2015, 2012; Merchant & Bartolo, 2017; Morillon & Baillet, 2017), accumulating evidence shows beta oscillation is associated with perceptual performance (Spitzer & Haegens, 2017), including detecting temporal or intensity deviations (Arnal, Doelling, & Poeppel, 2015; Herrmann, Henry, Haegens, & Obleser, 2016). Together, this suggests beta oscillation is important for forming temporal predictions, and may associate with the fidelity of perceptual processing.

Pitch is a fundamental perceptual feature of sound that is critical for identifying auditory objects and understanding speech and music, which are part of the *what* domain of auditory perception. Therefore, it is important to understand how auditory prediction for pitch is represented by neural oscillations.

We hypothesized that beta power modulation in auditory cortex co-represents both predictions of spectral frequency (*what*) and time (*when*), two essential dimensions of any auditory signal, consistent with the following evidence. First, neurons in primary auditory cortex are selectively tuned to both spectral and temporal aspects of sound (Boemio, Fromm, Braun, & Poeppel, 2005; Fritz, Shamma, Elhilali, & Klein, 2003; King & Nelken, 2009; Lakatos et al., 2013; Schönwiesner and Zatorre, 2009). Second, beta oscillation is associated with communication between auditory and motor areas (Fujioka et al., 2012), and premotor cortex is activated by spectral as well as temporal predictions (Schubotz, 2007). Third, induced beta power recorded from human auditory cortex is associated with updating pitch prediction, as beta power is modulated by prediction error or prediction updating after the onset of an unpredicted sensory event (Chang, Bosnyak, & Trainor, 2016; El Karoui et al., 2015; Sedley et al., 2016). However, these studies did not report whether there is an effect of prediction on beta power prior to the stimulus onset, and thus it is unclear whether beta power reflects anticipatory sensory prediction. The current study aimed to overcome this lack of knowledge by investigating beta power prior to a pitch change.

The P3a component of the event-related potential (ERP) is regarded as an index of prediction error, and thus it can be used to access whether an auditory event is successfully predicted. When participants passively listen to a sequence of repeated tones with infrequent deviants, both mismatch negativity (MMN) and P3a components of the ERP will be evoked by those deviants (Polich, 2007; Schröger et al., 2015). Although unpredictability usually covaries with rareness in a typical oddball paradigm, these two features can be dissociated and related to MMN and P3a differentially. The P3a amplitude reflects the magnitude of prediction error, as it is elicited by the unpredictability, but not the rareness, of the deviants (Max, Widmann, Schröger, & Sussman, 2015; Sussman, Winkler, & Schröger, 2003). In contrast, the MMN amplitude reflects local rareness rather than unpredictability (e.g., Bekinschtein et al., 2009). Therefore, we hypothesized that, if beta power modulation in auditory cortex reflects sensory prediction, it should attenuate the prediction error response (i.e., P3a amplitude).

The current study investigated whether beta power modulation, which reflects predictive timing, is also modulated by the predictability of an occasional pitch change. We employed two isochronous (temporally predictable) auditory oddball sequences with 20% of the tones being at a different (deviant) pitch from the standard tones. The deviant pitches were presented every fifth tone in one sequence (Predictable sequence), but the deviant and standard pitches were pseudorandomly intermixed in the other sequence (Unpredictable sequence). We hypothesized that beta power modulation *prior* to deviant pitch onsets would be modulated by the predictability of the pitch change in the sequence. Furthermore, if beta power modulation reflects the predictability of pitch changes, a larger beta power modulation (i.e., desynchronization depth) should occur prior to the onset of more successfully predicted deviant pitches. Therefore, in single-trial analyses using linear mixed-effect (LME) models, larger beta desynchronization depth immediately prior to a deviant should be associated with smaller deviant-evoked P3a amplitude, a neural response reflecting prediction error (Friston, 2005; Polich, 2007; Schröger et al., 2015).

2 Materials and methods

2.1 Participants

Seventeen participants were recruited from the McMaster University community, and 14 of them (18 – 27 years old, mean age 19.9 ± 2.4; 10 female) were used for data analyses (see 2.5.3 Artifact rejection for exclusion criterion). Participants were screened by a self-report survey to ensure they had normal hearing, were neurologically healthy and were right-handed. Signed informed consent was obtained from each participant. The McMaster University Research Ethics Board approved all procedures. Participants received course credit or reimbursement for completing the study.

2.2 Stimuli

Two recorded piano tones, C4 (262 Hz) and B4 (494 Hz), from the University of Iowa Musical Instrument Samples were used, with 10 msec rise times. Tones were truncated to 200 msec in duration, and a linear decay to zero was applied over the entire excerpt to remove offset artifact. The DC shift was removed for each tone. Sounds were converted into a monaural stream at 71 dB (C weighted), measured through an artificial ear (type 4152, Brüel & Kjær) with a sound level meter (type 2270, Brüel & Kjær). Sounds were delivered binaurally via ear inserts (Etymotic Research ER-2). All stimulus sequences were presented under the control of a digital signal processor (Tucker Davis RP2.1).

2.3 Procedure

The experiment was conducted in a sound-attenuated room. Each participant was presented with a continuous sequence of tones in each of two 30-min experimental sessions, while they watched a silent movie on a computer screen. Participants were instructed to sit comfortably and remain as still as possible during the experiment while watching a silent movie, and they were not required to make any responses, so that we could examine beta responses from auditory cortex without possible artifacts from muscle movement.

The tones were presented in oddball sequences, with the C4 tone as the standard and the B4 tone as the deviant. There were two sequence types, Predictable and Unpredictable, such that the only difference between them was whether the change from a standard pitch to a deviant pitch was predictable or not within the sequence. In the Predictable sequence, each deviant pitch was preceded by exactly 4 consecutive standard pitches, and this 5-tone pattern was cyclically repeated throughout the entire sequence, making the pitch of each tone in the sequence predictable. This manipulation has also been used in previous studies on the predictability of pitch changes (e.g., Dürschmid et al., 2016; Max et al., 2015; Schubotz, von Cramon, & Lohmann, 2003). In the Unpredictable sequence, the order of the standard and deviant pitches was pseudorandomized (with the only constraint being that two deviant pitches could not be presented sequentially), which made the pitch of subsequent tones largely unpredictable (only a standard immediately following a deviant was predictable, and these trials were excluded from analysis). The inter-onset interval (IOI) was fixed at 500 msec in both sequences, and each sequence contained 3600 tones, with a deviant occurrence rate of 20% (720 deviant tones). Although predictive coding has sometimes been studied in sequences with random IOI, we used a fixed IOI here as this reduces variability in beta modulation effects (e.g., Fujioka et al., 2012, 2009; Snyder & Large, 2005). An equal number of participants completed the Predictable or the Unpredictable sequence first. Participants took a three-minute break between experimental sessions.

The analyses on the interval preceding a deviant tone (preDEV trials) aimed to investigate whether beta desynchronization (power decrease) is modulated by the predictability of an upcoming pitch change. The analyses of deviant trials (DEV trials) examined neural responses to the occasional pitch changes. We also examined whether preDEV beta desynchronization depth was correlated with DEV trial responses to the pitch change. Only standard pitches between two other standard pitches were included in the analyses of standard pitches (STD trials), to avoid neural activity associated with deviant pitches (Fig. 1).

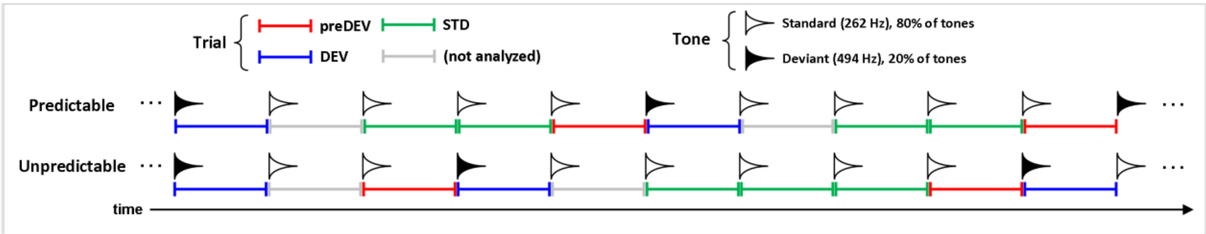

Fig. 1 The auditory sequences employed in current study. Two isochronous (IOI: 500 msec) tone sequences in which 80% of tones are at one pitch (standard F0: 262 Hz) and 20% are at a different pitch (deviant F0: 494 Hz). The only difference between sequences was that the deviant pitches were presented regularly every fifth tone in one sequence, making the pitch change predictable (Predictable condition), but the deviant and standard pitches were pseudorandomly intermixed in the other sequence, making the pitch change unpredictable (Unpredictable condition). According to their sequential position relative to the deviant pitch, the trials were categorized into preDEV (red interval), DEV (blue interval), and STD (green interval).

Given that we used only one IOI in an isochronous sequence, the current study does not fully replicate previous studies showing that beta power reflects predictive timing. Nevertheless, the results of analyses on beta power modulation on STD trials (shown in Supplementary Materials: S.1) are consistent with previous studies showing beta power entrains to temporal regularity reflecting predictive timing (e.g., Fujioka et al., 2012). Here we concentrate on beta power analyses related to predictive coding for expected pitches.

2.4 EEG recording

The EEG was sampled at 2048 Hz (filtered DC to 417 Hz) using a Biosemi Active Two amplifier (Biosemi B.V., Amsterdam). The 128-channel Biosemi pin-type active electrodes (Ag-AgCl) were placed based on geodesic partitioning of the head surface. The electrode array was digitized for each participant (Polhemus Fastrak) prior to recording. EEG data were transformed to an average reference offline.

2.5 Signal processing for source-space neural oscillatory activity

Three stages of signal processing were conducted in order to examine the behavior of auditory induced oscillations in bilateral auditory cortices, following Fujioka et al. (2012) and Chang et al. (2016). In the first stage, we obtained a dipole source model based on auditory ERP responses. The second stage segmented source waveforms into trials, categorized by whether they were STD, preDEV or DEV trials (Fig. 1). In the third stage, trials containing excessive artifacts were rejected.

2.5.1 Stage 1: Modeling auditory dipole sources with P1 component

We employed a dipole source model as a spatial filter in order to increase the signal-to-noise ratio of the EEG signal generated from left and right auditory cortices for subsequent analyses. In the present study, we were primarily interested in responses from auditory cortex, so we analyzed the EEG signals in source-space rather than from surface channels, extracting the oscillatory signals generated from left and right auditory cortices while attenuating signals generated from other brain regions (Scherg & Von Cramon, 1985). The continuous EEG data was band-pass filtered 1–20 Hz and then segmented into time periods −100 to 300 msec, time locked to stimulus onset. STD trials on which the amplitude ranged below 150 μV (i.e., low artifact) were averaged into ERP waveforms and used to model dipole sources. Two auditory cortex sources were estimated for each participant for the auditory evoked P1 (60–100 msec; Fig. 3) with the dipole locations constrained to be symmetric across hemispheres in location but not orientation, using the multiple source probe scan algorithm and the four-shell ellipsoid model included in the Brain Electrical Source Analysis (BESA) software package. P1 was chosen because it is the dominant peak at fast presentation rates (N1 peaks are strongly reduced at fast rates; Näätänen & Picton, 1987), and is generated primarily from primary auditory cortex (Godey, Schwartz, De Graaf, Chauvel, & Liegeois-Chauvel, 2001). The mean locations of fitted dipoles across participants were at Talairach coordinates [±45.8, −7.7, 17.7] with mean orientations [.3, .7, .7] and [−.2, .8, .6] for left and right dipoles, respectively. These locations are very close to bilateral primary auditory cortices with orientations toward the mid-frontal surface area, consistent with typical auditory evoked potentials. The residual variances of the source fittings for each participant ranged from 1.4 to 13.3%.

2.5.2 Stage 2: Trial segmentation

Based on individual participant dipole model fits, the auditory source waveforms of each trial at the left and right auditory cortical sources identified above were extracted for all trial types using signal space projection. Trials were segmented from −500 to 1000 msec, time-locked to the onset of the tone. Both the individual source waveform trials and raw 128-channel EEG data were exported from BESA to MATLAB for further processing.

2.5.3 Stage 3: Artifact rejection

For each segmented source waveform, the corresponding 128-channel data was examined for artifacts. The segments containing artifacts were eliminated from future analyses. The artifact rejection criteria (calculated on surface electrode waveforms) was to eliminate trials in which the amplitude range at any channel exceeded 40 μV for more than 10% of the 1500 msec trial length compared to the baseline mean voltage of the 100 msec prestimulus period for all trials. Three participants' data were excluded because too few trials (36–38%) were artifact-free. For the remaining participants (n = 14), 70.0 ± 13.8% (ranging from 50.6 to 90.9%) of the trials were accepted for further analyses.

2.6 Time-frequency decompositions

In order to remove the evoked (phase-locked) responses from the trial and thereby obtain the induced (non-phase-locked) responses for subsequent analyses on beta band, for each trial type, the source waveform was averaged as the estimation of the evoked response, and then subtracted from each single-trial source waveform (Chang et al., 2016; Fujioka et al., 2012; Kalcher & Pfurtscheller, 1995; Mouraux & Iannetti, 2008; Pfurtscheller, 2001; Pfurtscheller & Da Silva, 1999).

Time-frequency decompositions in the beta frequency band were calculated for each participant on each unfiltered single-trial source waveform separately in left and right auditory cortices using a Morlet wavelet transform (Bertrand, Bohorquez, & Pernier, 1994). The Morlet wavelet transformation was calculated on a window centered around each time point for each trial with 67 logarithmically-spaced frequency bins between 12 and 35 Hz. The wavelet was designed such that the half-maximum width was equal to 2.4 periods of the lowest frequency while the width was equal to 3.4 periods of the highest frequency, linearly interpolated for each frequency bin in between. Subsequently, 300 msec at the beginning and ending of each 1500 msec long trial were eliminated to avoid edge effects, the effectiveness of which was confirmed by visual inspection. The induced oscillatory power was calculated by averaging the power at each time-frequency point across trials. Induced power changes were expressed as a relative percentage, by normalizing the power of a trial to the mean power of the 0–500 msec time window of the STD trials for each frequency (Chang et al., 2016; Fujioka et al., 2012). For the preDEV trials, in order to focus on event-related spectral dynamics in the −500 to 0 msec period (time-locked to the deviant pitch onset), the percentage power was baseline corrected to the mean power of each frequency bin in the −700 to −600 msec period on the preDEV trials (equivalent to the −200 to −100 msec period time-locked to the preceding standard pitch onset).

To quantify the amplitude of desynchronization of the mean beta band (15–25 Hz) power, we measured the size of the negative peak within the interval −350 to −150 msec, time-locked to the onset of the deviant pitch. We chose this time window because it is in the middle of the 500 msec IOI, and we expected the maximum negative peak occur within this time window.

2.7 Signal processing for ERPs

For the analyses on trial-averaged ERP waveforms, the continuous EEG data for each electrode was .3–40 Hz band-pass filtered for each participant for each sequence, converted to a standard 81-channel montage in BESA, and then segmented into trials covering the time period −100 to 500 msec, time locked to stimulus onset, for the DEV and STD trials. We averaged across frontal midline (F1, Fz, and F2) and central midline (C1, Cz, and C2) montaged channels. The ERP waveform was baseline-corrected by subtracting the mean amplitude of the 100 msec prestimulus period.

In the ERP, we focused primarily on analyzing the amplitude of P3a, because previous studies have shown that it reflects the magnitude of prediction error (Max et al., 2015; Polich, 2007; Sussman et al., 2003) or a violation of the global regularity of a tone sequence (Bekinschtein et al., 2009; Faugeras et al., 2012). The P3a component is mainly observed over central midline (Polich, 2007), so P3a was analyzed at this location. In addition, we also analyzed the amplitude of the MMN at frontal midline, because it reflects an automatic preconscious response to occasional deviant pitches in a sequence, such as employed in the present study (Friedman, Cycowicz, & Gaeta, 2001; Näätänen, Paavilainen, Rinne, & Alho, 2007).

In order to accommodate potential individual differences in MMN and P3a latency (Conroy & Polich, 2007; Lieder, Daunizeau, Garrido, Friston, & Stephan, 2013), for each participant for each sequence, we first calculated the peak latency of the MMN and P3a in the difference ERP waveform (mean DEV – mean STD waveforms) in the time ranges 80–130 msec and 160–330 msec, respectively. In the second step, we estimated the amplitude of MMN and P3a by taking the area under the curve of the window of ±10 msec and ±20 msec, centered around the peak latencies of MMN and P3a, respectively. The ERP waveforms are corrected to the mean amplitude of the 100 msec prestimulus period.

The signal processing for extracting single-trial ERP waveforms was the same as the above with the following exceptions. First, the continuous EEG data was .3–7.0 Hz band-pass filtered, as a lowered cutoff frequency for the low-pass filter can increase the signal-to-noise ratio by attenuating the high frequency noise in single-trial ERP analysis (Heinrich et al., 2014; Spencer, 2005). Second, to quantify the single-trial ERP amplitude, the ERP difference waveform was extracted for each DEV trial by subtracting its preceding preDEV trial, so as to give a measure of the response to a deviant pitch relative its preceding context of standard pitches.

2.8 Single-trial correlation between beta desynchronization and P3a amplitude

To examine the trial-by-trial association between beta desynchronization depth on the preDEV trials and P3a amplitude on the DEV trials, we performed single-trial analyses using a LME model. LME modeling is an extension of linear regression modeling, which accesses the influence of predictors of interest (i.e., fixed effects), while taking into account variances across participants (i.e., random effects). In the current study, we were interested in whether P3a amplitude can be predicted by beta desynchronization amplitude (continuous variable) and sequence type (Predictable or Unpredictable; categorical variable). Both random intercepts and random slopes are included in our LME models, because this setup is known to have the best generalizability of the LME model (Barr, Levy, Scheepers, & Tily, 2013). Model fitting was implemented using the "lme4" package in R (Bates, Mächler, Bolker, & Walker, 2015), and the significance of the fixed effects was determined with type-II Wald tests using the "Anova" function in the "car" package in R (Fox & Weisberg, 2011).

2.9 Experimental design and statistical analysis

Participant (n = 14) was the random factor for the within-subject statistical tests in the current study. We employed planned non-parametric tests because the normality assumption was violated in many cases. The approximated test statistics (z-value) is reported for each test. The statistical tests were performed by MATLAB (2013a) or R (3.3.3). Statistical decisions were based on a two-tailed test.

3 Results

3.1 Predictability of pitch change modulates pre-deviant beta power

The main goal of this study was to test whether induced beta desynchronization is modulated by the predictability of the pitch of the upcoming tone. We analyzed the beta power activity across the interval preceding the onset of each deviant pitch (preDEV trials) in both the Predictable and Unpredictable sequences (Fig. 2), and we hypothesized that the predictability of the deviant pitch would modulate the induced beta power. We quantified the amplitude of desynchronization of the mean beta band (15–25 Hz) power by measuring the size of the negative peak within the interval of −350 to −150 msec, time-locked to the onset of the deviant pitch. In the right auditory cortex, Wilcoxon signed rank tests showed that the desynchronization was only significantly lower than 0 in the Predictable sequence ($z = -3.23$, $p < .001$), but not detectably different from 0 in the Unpredictable sequence ($z = -1.66$, $p = .104$). In the left auditory cortex, the desynchronization was not significantly different from 0 in either sequence (Predictable: $z = -1.73$, $p = .091$; Unpredictable: $z = -1.79$, $p = .079$). A Wilcoxon signed rank test showed that the desynchronization amplitude was more significantly negative in the Predictable sequence than the Unpredictable sequence in the right auditory cortex ($z = -2.17$, $p = .029$). However, there was no difference between Predictable and Unpredictable sequences in the left auditory cortex ($z = -.28$, $p = .808$).

We further explored whether the predictability of the pitch has different effects on low-beta (15–20 Hz) and high-beta (20–25 Hz) bands, as these two sub-bands could have different functions (e.g., Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013). However, we did not observe any differences between these two sub-bands. The detailed results are reported in Supplementary Materials: S.2 and Figure S2.

In sum, beta desynchronization was only observed prior to a deviant pitch in a predictable context but not in an unpredictable context. This is consistent with our hypothesis that predictability for *what* modulates beta power prior to a pitch change. In addition, the right-lateralization of the effect is consistent with the view that right auditory cortex is more sensitive for processing spectral information than is the left hemisphere (e.g., Chang et al., 2016; Zatorre et al., 1992, 2002).

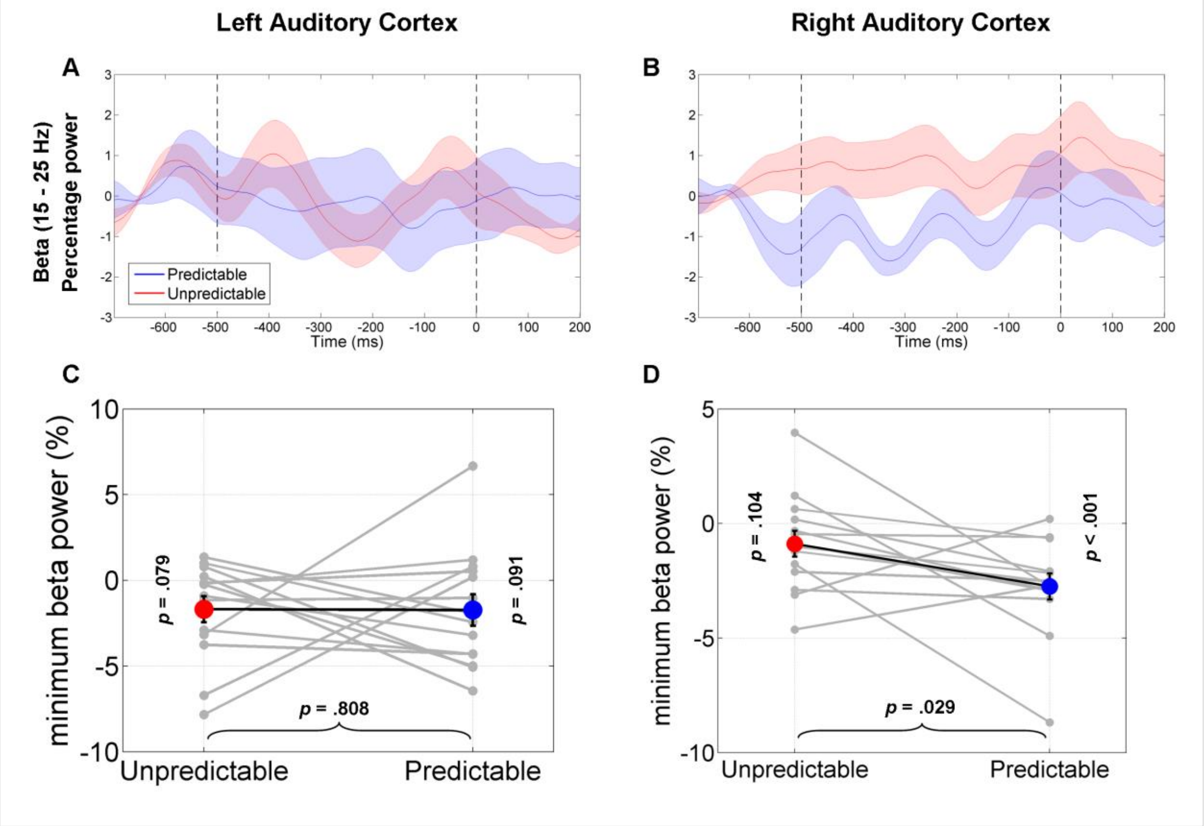

Fig. 2 Predictability of pitch change modulates pre-deviant beta power. The induced (non-phase-locked) oscillatory power was extracted from left (left panel) and right (right panel) auditory cortices using the dipole source model. (A and B) Beta (15–25 Hz) power was averaged across trials in each condition for each participant and are presented as the mean ± standard error across participants. The time-frequency maps of beta power on preDEV trials are shown in Figure S2. (C and D) The minimum beta power (desynchronization amplitude) in the −350 to −150 msec time window was extracted for each participant. The grey dots connected by a grey line represent the data points of each participant, and the red and blue dots and the error bars represent the conditional mean ± standard error. Wilcoxon signed rank tests showed that desynchronization was larger in Predictable than Unpredictable sequences in right auditory cortex, but not different in left auditory cortex.

3.2 Predictability of pitch change modulates deviant ERP amplitudes

We analyzed whether the deviant pitch evoked larger amplitudes of MMN and P3a ERP components in the Unpredictable than in the Predictable sequence (Fig. 3). MMN and P3a responses to occasional deviant tones have been well studied using auditory oddball sequences such as those in the present study (see Friedman et al., 2001; Polich, 2007 for reviews).

We first showed that MMN and P3a responses were observed in both sequences, as expected in a typical auditory oddball paradigm (Näätänen et al., 2007; Polich, 2007). The analyses on the average of frontal midline electrodes using Wilcoxon signed rank tests showed that for both sequence types, the amplitudes of MMN ($z = -3.30$, $p < .001$ in both sequences) and P3a components ($z = 3.30$, $p < .001$ in Predictable sequences; $z = 2.86$, $p = .002$ in Unpredictable sequences), were significantly different from zero in the difference waveforms (DEV minus STD trials). Similar results were found for the same analyses on the average of central midline electrodes: the amplitudes of MMN (z = −3.30, *p* < .001 in both sequences) and P3a components (z = 3.30, *p* < .001 in both sequences) were significantly different from zero in the difference waves for both Predictable and Unpredictable sequences.

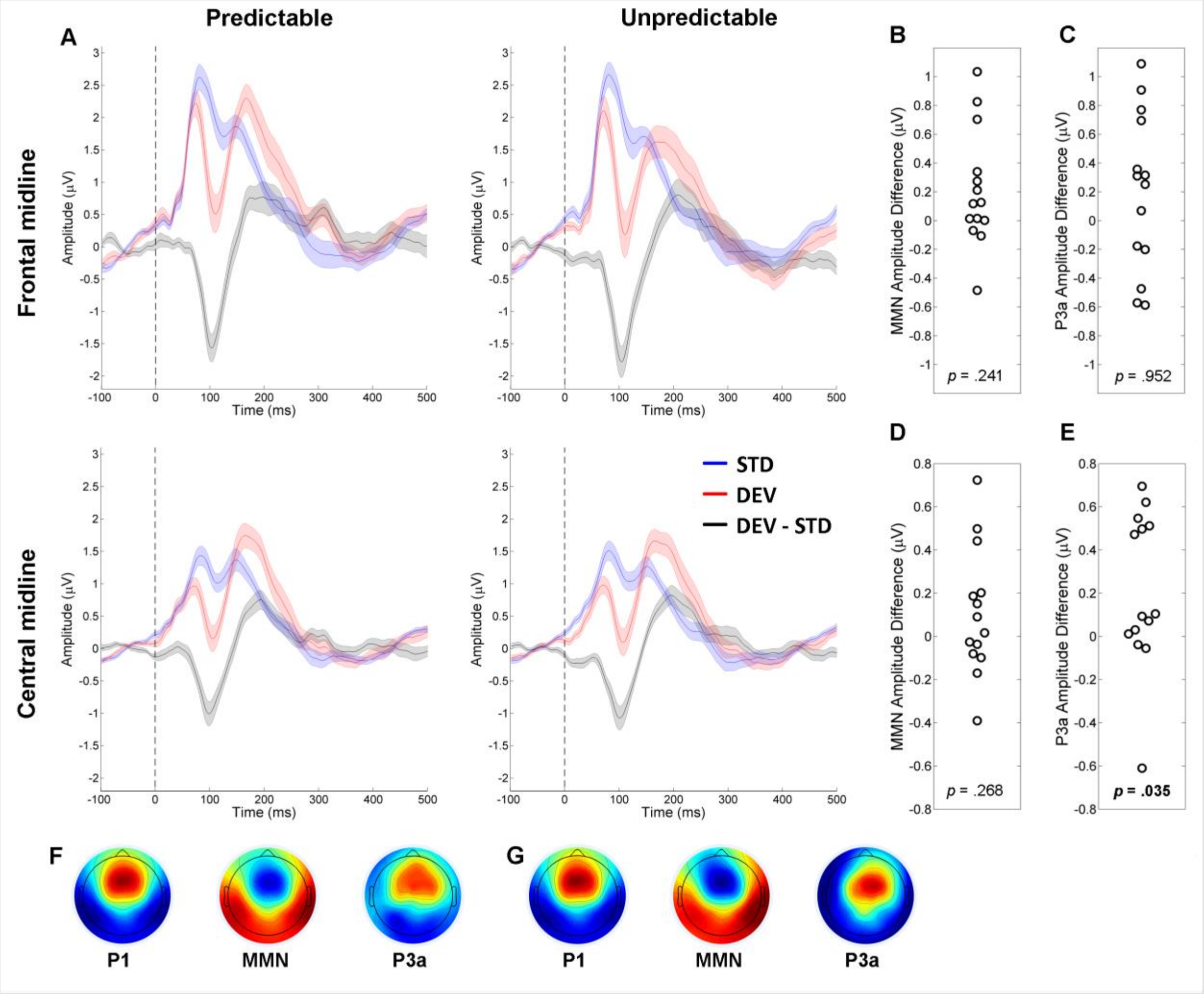

Fig. 3 Predictability of pitch change modulates deviant ERP amplitudes. (A) The ERP waveforms of STD (blue) and DEV (red), and the difference waveform (DEV – STD [black]) in Predictable and Unpredictable sequences at frontal midline and central midline electrodes. ERP waveforms are presented as the mean ± standard error across participants. (B, C, D and E) The amplitude differences (Unpredictable sequence minus Predictable sequence) for MMN (left panel) and P3a (right panel), where each circle represents the amplitude difference of one participant at frontal midline electrodes (upper panel) and at central midline electrodes (lower panel). Wilcoxon signed rank tests showed that only the P3a amplitude in central midline electrodes were significantly larger in the Unpredictable sequence than Predictable sequence. (F and G) ERP component topographies (grand-averaged across participants), including P1, MMN and P3a for the (F) Predictable and (G) Unpredictable sequences. The highest amplitude is presented as red, the lowest amplitude is presented as blue, with a symmetrical range around zero (green).

More interesting, we further investigated whether the predictability of the deviants modulated subsequent MMN or P3a. At the frontal midline average, Wilcoxon signed rank tests did not show any differences in either MMN (z = 1.22, *p* = .241, Fig. 3B) or P3a (peak-to-peak corrected to mean MMN amplitude, z = −.09, *p* = .952, Fig. 3C) between Predictable and Unpredictable sequences. At the central midline average, Wilcoxon signed rank tests did not show a significant difference in MMN amplitude between sequences (z = 1.16, *p* = .268, Fig. 3D). On the other hand, the mean P3a amplitude was larger in the Unpredictable sequence than the Predictable sequence (z = 2.10, *p* = .035, Fig. 3E; if the P3a Amplitude Difference outlier [−.61; exceeding 2.28 standard deviations from the mean] was excluded, then z = 2.69, *p* = .005).

Together, these results suggest that the predictability of a deviant pitch modulates P3a amplitude but not MMN amplitude, such that unpredictable deviant pitches (generating a prediction error) elicit higher attentional capture compared to predictable deviant pitches, replicating previous studies (Max et al., 2015; Polich, 2007; Sussman et al., 2003). The results are also consistent with previous findings that MMN is sensitive to local deviance occurrence rates (e.g., Bekinschtein et al., 2009; Faugeras et al., 2012); in the current study, local deviance occurrence rates were equivalent in the two conditions (20%) and MMN did not differ between conditions.

3.3 Pre-deviant beta power is associated with deviant P3a amplitude

The above analyses, by comparing experimental conditions, showed that the predictability of a deviant pitch in a tone sequence context modulates both the pre-deviant (preDEV trial) induced beta power activity in the right auditory cortex and the deviant P3a amplitude at the central midline average. We thus examined whether these two neural activities are correlated at the trial-by-trial level.

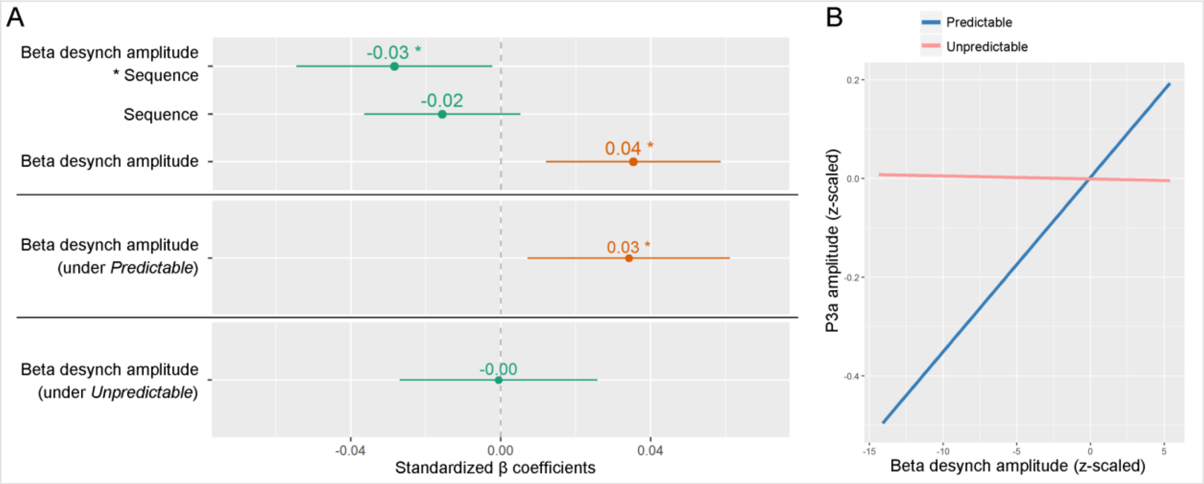

Fig. 4 Pre-deviant beta power depth correlates with deviant P3a amplitude when pitch change is predictable. We used LME models to examine the trial-by-trial relationship between beta desynchronization depth (negative peak) on preDEV trials and P3a amplitude on the following DEV trials. The visualization was implemented by the "sjPlot" package in R (Lüdecke, 2016). (A) The best fitted standardized β coefficients (fixed-effects only). In the upper panel, "Sequence" indicates differences in the effect of Unpredictable versus Predictable sequences on P3a amplitude, "Beta desynch amplitude" indicates the effect of beta desynchronization amplitude on P3a amplitude, and "Beta desynch amplitude * Sequence" indicates the interaction effect of these two variables on P3a amplitude. In the middle and lower panels, the effect of beta desynchronization amplitude on P3a amplitude was analyzed under each of Predictable and Unpredictable sequences. The dot and error bar represent the standardized β (fixed-effect coefficient) and 95% confidence interval, with * $p < .05$. (B) The predicted relationship between beta desynchronization amplitude and P3a amplitude, under each of Predictable and Unpredictable sequences, based on the LME model. The x and y axes are z-scaled for visualization. In sum, the individual trial analyses showed that deeper pre-deviant beta desynchronization depth (power decrease) was followed by lower deviant-evoked P3a amplitude in the sequence with predictable pitch changes.

We performed a single-trial analysis with linear mixed effect (LME) models of whether the P3a amplitude can be predicted by beta desynchronization amplitude (negative peak), and whether this relationship is modulated by Predictable or Unpredictable sequences (Fig. 4A). The initial LME model showed a significant interaction effect between beta desynchronization amplitude and the type of sequence [standardized $\beta = -.029$, standardized SE = .013, $\chi 2(1) = 4.56$, $p = .032$]. We thus further analyzed the LME model within each Predictable or Unpredictable sequence. The results showed a significant positive relationship between beta desynchronization amplitude and P3a amplitude for the Predictable sequence [standardized $\beta = .034$, standardized SE = .014, $\chi 2(1) = 6.13$, $p = .013$]; however, the effect was not significant for the Unpredictable sequence [standardized $\beta = -5.4*10^{-4}$, standardized SE = .013, $\chi 2(1) = .002$, $p = .968$].

Together, the trial-by-trial analyses showed that deeper beta desynchronization depth (lower beta power amplitude) preceded trials with smaller deviant-evoked P3a amplitude in sequences where pitch changes were predictable (Fig. 4B). Increased post-processing (P3a amplitude) is indicative of a failure to predict the pitch change. Thus, greater beta desynchronization prior to a pitch deviant appears to enhance the predictability of the upcoming pitch deviant, resulting in a smaller prediction error response following the pitch deviant.

4 Discussion

The current study aimed to investigate whether power modulation of induced beta oscillation (15–25 Hz) in auditory cortices reflects spectral in additional to temporal prediction. To manipulate the predictability of pitch changes while controlling temporal predictability, we employed two isochronous auditory oddball sequences, where both sequences were presented at the same presentation speed and the same deviant pitch occurrence rate (20%). The only difference was that the deviant pitch occurred regularly every fifth tone in the predictable sequence but was pseudorandomly intermixed with standard pitches in the unpredictable sequence.

We report the novel finding that the predictability of a pitch change modulates beta power immediately prior to a deviant pitch onset. Specifically, we found that beta desynchronization was deeper prior to the onset of a predictable deviant pitch than an unpredictable one. Furthermore, a trial-by-trial LME analysis showed that within the predictable sequence, the deeper the beta desynchronization prior to a deviant pitch, the smaller the P3a amplitude evoked by that deviant pitch. This result indicates that even when the same stimulus is presented on different trials, deeper beta desynchronization depth prior to the stimulus is associated with better prediction of pitch change. To the best of our knowledge, while previous reports indicate that beta oscillations reflect temporal prediction, this is the first report that auditory beta modulation depth reflects sensory prediction of *what* is expected next.

We demonstrated that P3a amplitude, but not MMN amplitude, was larger in the Unpredictable than in the Predictable sequence, consistent with previous findings that predictability of a tone sequence modulate deviant-evoked P3a amplitude (Max et al., 2015; Sussman et al., 2003). Studies have shown that P3a reflects involuntary attentional capturing, elicited by unpredicted deviant stimuli, even when task-irrelevant (Friedman et al., 2001; Polich, 2007; Rinne, Särkkä, Degerman, Schröger, & Alho, 2006; Schröger et al., 2015, 2000; Sussman et al., 2003; Wetzel, Schröger, & Widmann, 2013). For example, ERP studies have shown that unpredictable task-irrelevant pitch changes elicit P3a responses, but that such P3a responses are eliminated when the pitch change is predictable, either cued by the regularity of a sequence (e.g., every fifth tone) or by a visual cue (Max et al., 2015; Sussman et al., 2003). Also, other studies manipulating pitch regularity in tone sequences in global and local hierarchies showed that MMN amplitude responds to locally rare pitch and P3 amplitude responds to violations of global pitch regularity (e.g., Bekinschtein et al., 2009; Dürschmid et al., 2016; Faugeras et al., 2012). It's important to note that these ERP effects might depend on the listening tasks being used in the experiment, as the MMN amplitude can reflect the global pitch regularity (predictability) when participants are required to attend to the sound (e.g., Wacongne et al., 2011), which is different from the passive listening paradigm of the current study. Together, the association between beta desynchronization and P3a amplitude found in the current study is consistent with the interpretation that deeper beta desynchronization reflects more successful prediction of upcoming pitch changes, and thus reduces exogenous drawing of attention toward unpredicted events (Friston, 2005; Polich, 2007; Schröger et al., 2015).

There is a debate as to whether the desynchronization response of beta power modulation reflects predictive or a reactive mechanism (Teki & Kononowicz, 2016). The predictive coding framework hypothesizes that beta power modulation reflects prediction of the upcoming event (Arnal & Giraud, 2012) while the reactive event tagging framework hypothesizes that beta oscillation reflects the memory encoding of a perceived salient event (Hanslmayr & Staudigl, 2014; Teki & Griffiths, 2014, 2016). Previous studies were unable to distinguish these alternative hypotheses, given that they used metrically accented tones that occurred cyclically along the sequence (Fujioka et al., 2015; Iversen, Repp, & Patel, 2009; Snyder & Large, 2005), and the shortest temporal distance between two down-beats was 800 msec, making it even more difficult to distinguish whether the beta desynchronization reflected prediction of an upcoming stimulus or reaction to the preceding stimulus. We solved the cyclical issue by comparing sequences with and without pattern regularity. Under this manipulation, the current study showed that beta desynchronization is anticipatorily associated with pitch change only in the predictable context but not in the unpredictable context, which supports the idea that beta desynchronization reflects predictive coding. However, we do not exclude the possibility that event tagging processes are represented as another pattern of activity in beta band. Studies to date suggest that beta oscillation can be subdivided into high (>20 Hz) and low (<20 Hz) bands, which might be related to different functions (Kilavik et al., 2013; Spitzer & Haegens, 2017). Specifically, novel auditory or visual stimuli elicit subsequent activity in the low-beta band (e.g., Chang, Ide, Li, Chen, & Li, 2017, Chang et al., 2016; Fujioka, Trainor, Large, & Ross, 2009; Haenschel, Baldeweg, Croft, Whittington, & Gruzelier, 2000), and these effects are consistent with the event tagging framework. Therefore, we suggest that the desynchronization of the entire beta band reflects predictive processes, while the low-beta power increase after an unexpected pitch might relate more specifically to an event-tagging process.

The view that beta oscillation reflects sensory prediction is consistent with predictive coding theory, as more salient beta modulation is associated with attenuated P3a amplitude. A successfully predicted sensory input elicits smaller subsequent attentional responses, which are responsible for propagating error signals in brain networks for further updating sensory prediction (Arnal & Giraud, 2012; Friston, 2005, 2009; Heilbron & Chait, 2017; den Ouden, Kok, & De Lange, 2012; Hohwy, 2012; Kopell, Whittington, & Kramer, 2011; Schröger et al., 2015). Also, beta oscillation has been proposed to reflect the cortical representation of maintenance or reactivation of the perceived sensorimotor or cognitive state (Engel & Fries, 2010; Spitzer & Haegens, 2017), which is the basis for predicting upcoming events. A limitation of the current study is that we did not orthogonally manipulate pitch prediction and prediction precision (inverse variance of prediction), which are dissociable factors in predictive coding theory, and thus we are unable to further distinguish whether beta power modulation reflects one or both of these processes. However, a recent study, which recorded local field potentials from human auditory cortex while participants listened to sequences with varied pitches, found that post-stimulus induced beta power was associated with updating spectral prediction but not prediction precision (Sedley et al., 2016). Although this association was only observed in the post-stimulus period and not in the pre-stimulus period (Sedley et al., 2016), it favors the explanation that the pre-deviant beta power modulation in the current study reflects prediction rather than prediction precision.

It is important to note that the standard and deviant pitches in the current study were 11 semitones apart. Considering the tonotopic organization of auditory cortex, it is likely that the reported beta oscillations were generated by different neuron ensembles tuned to standard or deviant pitch (cf., Lakatos et al., 2013). Thus, because the pitch change occurred regularly every fifth tone of the Predictable sequence (.4 Hz), an alternative explanation of the beta power modulation effect is that the neuron ensemble tuned to the deviant pitch frequency independently entrained to the rhythmic inter-deviant interval in the Predictable sequence (.4 Hz). In other words, there is a potential confound between timing and pitch expectations, and the beta power modulation might reflect predictive timing of deviant tone onsets rather than, or in addition to, predictive coding of pitch changes. However, we argue that it is unlikely to be the case. Perceptual and sensorimotor evidence shows that rhythm tracking performance becomes imprecise for tempos slower than .5 Hz (see Repp, 2005 for a review), and neural oscillatory evidence shows that neural entrainment activities cannot be robustly observed for tempos slower than 1 Hz (Doelling & Poeppel, 2015). The inter-deviant interval rate (.4 Hz) in the Predictable sequence of the current study was slower than these limits, and thus the deviant tempo alone, if processed in a separate channel and not nested within the 2 Hz tone sequence, is unlikely to be tracked. Therefore, we propose that the neuron ensembles tuned to different pitch frequencies might be interconnected and form a predictive coding network in the auditory cortex, and beta oscillation might play an important role in this (cf., Wang, 2010). We acknowledge that the current evidence is only in favor of the explanation that beta oscillatory power reflects the predictability of a pitch change (the *what* domain), and the current experimental design is insufficient to completely rule out the alternative explanations, as the predictability of what and when are not fully dissociated. Further electrophysiological evidence is needed to fully test this hypothesis.

The current findings also extend our understanding of the function of beta oscillation in sensory processing. First, predictions for both what and when are essential for processing dynamic auditory information, and beta oscillation likely plays an important role in these processes as it co-represents both prediction types. In particular, prediction is essential for auditory stream segregation and chunking the input into hierarchical meaningful segments (Wacongne et al., 2011; Winkler et al., 2009), which are required for perceiving speech and music (Hickok, 2012; Hickok & Poeppel, 2007; Sridharan, Levitin, Chafe, Berger, & Menon, 2007) among other sounds. For example, speech must be hierarchically segmented into phonemes, words and phrases; music must be segmented into subphrases and phrases. Second, sensory predictions reflected by beta power modulation might subsequently be associated with improved perception, via top-down controlling of attentional gain (Lee, Whittington, & Kopell, 2013; Morillon & Baillet, 2017). This is consistent with previous auditory studies showing that prestimulus beta power is higher when participants make correct compared to incorrect judgments at detecting temporal deviation (Arnal et al., 2015), detecting intensity deviation in tone sequences (Herrmann et al., 2016), detecting distorted pitch in music (Doelling & Poeppel, 2015), or discriminating frequency and intensity (Kayser, McNair, & Kayser, 2016). Third, the current finding of a relation between beta oscillation and sensory prediction can potentially be generalized to other sensory modalities. It has been proposed that beta oscillation plays a role in updating prediction in micro-scale neural circuits (e.g., Arnal & Giraud, 2012; Wang, 2010), and it is possible that such neural circuit exist in other cortical sensory regions. This idea is supported by previous studies showing that beta oscillation is associated with predicting tactile stimuli (van Ede, Jensen, & Maris, 2010), predicting spatial-temporal properties of the visual stimuli (Heideman, Ede, & Nobre, 2017), and motor planning for music performance (Bianco, Novembre, Keller, Villringer, & Sammler, 2018).

Previous studies indicate that the motor system is involved in predicting and perceiving temporal (e.g., Chen, Penhune, & Zatorre, 2008, 2006; Fujioka et al., 2012; Grahn, 2012; Grahn & Brett, 2007; Grube et al., 2010; Manning & Schutz, 2013; McAuley, Henry, & Tkach, 2012; Morillon, Schroeder, & Wyart, 2014; Phillips-Silver & Trainor, 2005; Schubotz, Friederici, & von Cramon, 2000; Schubotz & von Cramon, 2001; Teki, Grube, Kumar, & Griffiths, 2011, but see; Meijer, te Woerd, & Praamstra, 2016) and spectral (Schubotz, 2007; Schubotz & von Cramon, 2002; Schubotz et al., 2003) aspects of auditory sequences. Our finding that beta oscillation reflects pitch prediction as well as temporal prediction is consistent with the general idea that the sensory prediction process involves interactions between sensory and motor areas (Arnal, 2012; Grahn, 2012; Iversen & Balasubramaniam, 2016), given that beta oscillation has been suggested to reflect network communication between auditory and motor regions (Bartolo & Merchant, 2015; Fujioka et al., 2012; Kilavik et al., 2013; Merchant & Bartolo, 2017; Morillon & Baillet, 2017).

5 Conclusions

The current study shows that oscillatory beta power desynchronization is deeper prior to a predictable pitch change than an unpredictable change, indicating that beta power modulation reflects predictability for what is expected to happen as well as when it will happen. Our further trial-by-trial analysis showed that deeper beta power modulation prior to a pitch change is correlated with reduced attention-capturing prediction error responses (P3a amplitude) following the pitch change, demonstrating the link between sensory prediction and subsequent attentional processes. Together with previous studies, beta-frequency oscillations reflect predictive aspects of spectral and temporal processing that are critical for processing dynamic auditory streams, such as speech and music.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cortex.2018.06.008.

References

Arnal L.H., Predicting “when” using the motor system's beta-band oscillations, *Frontiers in Human Neuroscience* **6**, 2012, 225.

Arnal L.H., Doelling K.B. and Poeppel D., Delta–beta coupled oscillations underlie temporal prediction accuracy, *Cerebral Cortex* **25**, 2015, 3077–3085.

Arnal L.H. and Giraud A.L., Cortical oscillations and sensory predictions, *Trends in Cognitive Science* **16**, 2012, 390–398.

Barr D.J., Levy R., Scheepers C. and Tily H.J., Random effects structure for confirmatory hypothesis testing: Keep it maximal, *Journal of Memory and Language* **68**, 2013, 255–278.

Bartolo R. and Merchant H., β oscillations are linked to the initiation of sensory-cued movement sequences and the internal guidance of regular tapping in the monkey, *Journal of Neuroscience* **35**, 2015, 4635–4640.

Bates D., Mächler M., Bolker B. and Walker S., Fitting linear mixed-effects models using lme4, *Journal of Statistical Software* **67**, 2015, 1–48.

Bekinschtein T.A., Dehaene S., Rohaut B., Tadel F., Cohen L. and Naccache L., Neural signature of the conscious processing of auditory regularities, *Proceedings of the National Academy of Sciences of the USA* **106**, 2009, 1672–1677.

Bertrand O., Bohorquez J. and Pernier J., Time-frequency digital filtering based on an invertible wavelet transform: An application to evoked potentials, *IEEE T Bio-Medical Engineering* **41**, 1994, 77–88.

Bianco R., Novembre G., Keller P.E., Villringer A. and Sammler D., Musical genre-dependent behavioural and EEG signatures of action planning. A comparison between classical and jazz pianists, *Neuroimage* **169**, 2018, 383–394.

Boemio A., Fromm S., Braun A. and Poeppel D., Hierarchical and asymmetric temporal sensitivity in human auditory cortices, *Nature Neuroscience* **8**, 2005, 389–395.

Chang A., Bosnyak D.J. and Trainor L.J., Unpredicted pitch modulates beta oscillatory power during rhythmic entrainment to a tone sequence, *Frontiers in Psychology* **7**, 2016, 327.

Chang A., Ide J.S., Li H.H., Chen C.C. and Li C.S.R., Proactive control: Neural oscillatory correlates of conflict anticipation and response slowing, *eNeuro 4 – ENEURO.0061–0117.2017* 2017, https://doi.org/10.1523/ENEURO.0061-17.2017.

Chang A., Livingstone S.R., Bosnyak D.J. and Trainor L.J., Body sway reflects leadership in joint music performance, *Proceedings of the National Academy of Sciences of the USA* **114**, 2017, E4134–E4141, https://doi.org/10.1073/pnas.1617657114.

Chen J.L., Penhune V.B. and Zatorre R.J., Listening to musical rhythms recruits motor regions of the brain, *Cerebral Cortex* **18**, 2008, 2844–2854.

Chen J.L., Zatorre R.J. and Penhune V.B., Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms, *Neuroimage* **32**, 2006, 1771–1781.

Cirelli L.K., Bosnyak D., Manning F.C., Spinelli C., Marie C., Fujioka T., et al., Beat-induced fluctuations in auditory cortical beta-band activity: Using EEG to measure age-related changes, *Frontiers in Psychology* **5**, 2014, 742.

Conroy M.A. and Polich J., Normative variation of P3a and P3b from a large sample: Gender, topography, and response time, *Journal of Psychophysiology* **21**, 2007, 22–32.

den Ouden H.E., Kok P. and De Lange F.P., How prediction errors shape perception, attention, and motivation, *Frontiers in Psychology* **3**, 2012, 548.

Doelling K.B. and Poeppel D., Cortical entrainment to music and its modulation by expertise, *Proceedings of the National Academy of Sciences of the USA* **112**, 2015, E6233–E6242.

Dürschmid S., Edwards E., Reichert C., Dewar C., Hinrichs H., Heinze H.J., et al., Hierarchy of prediction errors for auditory events in human temporal and frontal cortex, *Proceedings of the National Academy of Sciences of the USA* **113**, 2016, 6755–6760.

El Karoui I., King J.R., Sitt J., Meyniel F., Van Gaal S., Hasboun D., et al., Event-related potential, time-frequency, and functional connectivity facets of local and global auditory novelty processing: An intracranial study in humans, *Cerebral Cortex* **25**, 2015, 4203–4212.

Engel A.K. and Fries P., Beta-band oscillations—signalling the status quo?, *Current Opinion in Neurobiology* **20**, 2010, 156–165.

Faugeras F., Rohaut B., Weiss N., Bekinschtein T., Galanaud D., Puybasset L., et al., Event related potentials elicited by violations of auditory regularities in patients with impaired consciousness, *Neuropsychologia* **50**, 2012, 403–418.

Fox J. and Weisberg S., An R companion to applied regression, 2011, Sage Publications.

Friedman D., Cycowicz Y.M. and Gaeta H., The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty, *Neuroscience in Biobehavioral Reviews* **25**, 2001, 355–373.

Friston K., A theory of cortical responses, *Philosophical Transactions of the Royal Society of London B – Biological* **360**, 2005, 815–836.

Friston K., The free-energy principle: A rough guide to the brain?, *Trends in Cognitive Science* **13**, 2009, 293–301.

Fritz J., Shamma S., Elhilali M. and Klein D., Rapid task-related plasticity of spectrotemporal receptive fields in primary auditory cortex, *Nature Neuroscience* **6**, 2003, 1216–1223.

Fujioka T., Ross B. and Trainor L.J., Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery, *Journal of Neuroscience* **35**, 2015, 15187–15198.

Fujioka T., Trainor L.J., Large E.W. and Ross B., Beta and gamma rhythms in human auditory cortex during musical beat processing, *Annals of the New York Academy of Sciences* **1169**, 2009, 89–92.

Fujioka T., Trainor L.J., Large E.W. and Ross B., Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations, *Journal of Neuroscience* **32**, 2012, 1791–1802.

Godey B., Schwartz D., De Graaf J.B., Chauvel P. and Liegeois-Chauvel C., Neuromagnetic source localization of auditory evoked fields and intracerebral evoked potentials: A comparison of data in the same patients, *Clinical Neurophysiology* **112**, 2001, 1850–1859.

Grahn J.A., Neural mechanisms of rhythm perception: Current findings and future perspectives, *Topics in Cognitive Science* **4**, 2012, 585–606.

Grahn J.A. and Brett M., Rhythm and beat perception in motor areas of the brain, *Journal of Cognitive Neuroscience* **19**, 2007, 893–906.

Grube M., Cooper F.E., Chinnery P.F. and Griffiths T.D., Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration, *Proceedings of the National Academy of Sciences of the USA* **107**, 2010, 11597–11601.

Haenschel C., Baldeweg T., Croft R.J., Whittington M. and Gruzelier J., Gamma and beta frequency oscillations in response to novel auditory stimuli: A comparison of human electroencephalogram (EEG) data with in vitro models, *Proceedings of the National Academy of Sciences of the USA* **97**, 2000, 7645–7650.

Hanslmayr S. and Staudigl T., How brain oscillations form memories—a processing based perspective on oscillatory subsequent memory effects, *Neuroimage* **85**, 2014, 648–655.

Heideman S.G., Ede F. and Nobre A.C., Temporal alignment of anticipatory motor cortical beta lateralisation in hidden visual-motor sequences, *European Journal of* Neuroscience Advance online publication 2017.

Heilbron M, Chait M., (in press) Great expectations: Is there evidence for predictive coding in auditory cortex? Neuroscience Advance online publication 2017.

Heinrich H., Busch K., Studer P., Erbe K., Moll G.H. and Kratz O., Refining the picture of reduced alerting responses in ADHD–A single-trial analysis of event-related potentials, *Neuroscience Letters* **582**, 2014, 49–53.

Henry M.J., Herrmann B. and Obleser J., Entrained neural oscillations in multiple frequency bands comodulate behavior, *Proceedings of the National Academy of Sciences of the USA* **111**, 2014, 14935–14940.

Henry M.J. and Obleser J., Frequency modulation entrains slow neural oscillations and optimizes human listening behavior, *Proceedings of the National Academy of Sciences of the USA* **109**, 2012, 20095–20100.

Herrmann B., Henry M.J., Haegens S. and Obleser J., Temporal expectations and neural amplitude fluctuations in auditory cortex interactively influence perception, *Neuroimage* **124**, 2016, 487–497.

Hickok G., The cortical organization of speech processing: Feedback control and predictive coding the context of a dual-stream model, *Journal of Communication Disorders* **45**, 2012, 393–402.

Hickok G., Farahbod H. and Saberi K., The rhythm of perception: Entrainment to acoustic rhythms induces subsequent perceptual oscillation, *Psychological Science* **26**, 2015, 1006–1013.

Hickok G. and Poeppel D., The cortical organization of speech processing, *Nature Reviews Neuroscience* **8**, 2007, 393–402.

Hohwy J., Attention and conscious perception in the hypothesis testing brain, *Frontiers in Psychology* **3**, 2012, 96.

Iversen J.R. and Balasubramaniam R., Synchronization and temporal processing, *Current Opinion in Behavioral Sciences* **8**, 2016, 175–180.

Iversen J.R., Repp B.H. and Patel A.D., Top-down control of rhythm perception modulates early auditory responses, *Annals of the New York Academy of Sciences* **1169**, 2009, 58–73.

Kalcher J. and Pfurtscheller G., Discrimination between phase-locked and non-phase-locked event-related EEG activity, *Electroencephalography and Clinical Neurophysiology* **94**, 1995, 381–384.

Kayser S.J., McNair S.W. and Kayser C., Prestimulus influences on auditory perception from sensory representations and decision processes, *Proceedings of the National Academy of Sciences of the USA* **113**, 2016, 4842–4847.

Kilavik B.E., Zaepffel M., Brovelli A., MacKay W.A. and Riehle A., The ups and downs of beta oscillations in sensorimotor cortex, *Experimental Neurology* **245**, 2013, 15–26.

King A.J. and Nelken I., Unraveling the principles of auditory cortical processing: Can we learn from the visual system?, *Nature Neuroscience* **12**, 2009, 698–701.

Kopell N., Whittington M.A. and Kramer M.A., Neuronal assembly dynamics in the beta1 frequency range permits short-term memory, *Proceedings of the National Academy of Sciences of the USA* **108**, 2011, 3779–3784.

Kragness H. and Trainor L., Listeners lengthen phrase boundaries in self-paced music, *Journal of Experimental Psychology – Human Perception and Performance* **42**, 2016, 1676–1686.

Kragness H. and Trainor L., Young children pause on phrase boundaries in self-paced music listening: The role of harmonic cues, *Developmental Psychology* **54**, 2018, 842-856.

Lakatos P., Musacchia G., O'Connel M.N., Falchier A.Y., Javitt D.C. and Schroeder C.E., The spectrotemporal filter mechanism of auditory selective attention, *Neuron* **77**, 2013, 750–761.

Large E.W. and Jones M.R., The dynamics of attending: How people track time-varying events, *Psychological Review* **106**, 1999, 119–159.

Lee J.H., Whittington M.A. and Kopell N.J., Top-down beta rhythms support selective attention via interlaminar interaction: A model, *Plos Computational Biology* **9**, 2013, e1003164.

Lieder F., Daunizeau J., Garrido M.I., Friston K.J. and Stephan K.E., Modelling trial-by-trial changes in the mismatch negativity, *Plos Computational Biology* **9**, 2013, e1002911.

Lüdecke D., sjPlot: Data visualization for statistics in social science, R package version2016.

Manning F. and Schutz M., “Moving to the beat” improves timing perception, *Psychonomic Bulletin and Review* **20**, 2013, 1133–1139.

Max C., Widmann A., Schröger E. and Sussman E., Effects of explicit knowledge and predictability on auditory distraction and target performance, *International Journal of Psychophysiology* **98**, 2015, 174–181.

McAuley J.D., Henry M.J. and Tkach J., Tempo mediates the involvement of motor areas in beat perception, *Annals of the New York Academy of Sciences* **1252**, 2012, 77–84.

Meijer D., te Woerd E. and Praamstra P., Timing of beta oscillatory synchronization and temporal prediction of upcoming stimuli, *Neuroimage* **138**, 2016, 233–241.

Merchant H. and Bartolo R., Primate beta oscillations and rhythmic behaviors, *Journal of Neural Transmission* **124**, 2017, 1–10.

Morillon B. and Baillet S., Motor origin of temporal predictions in auditory attention, *Proceedings of the National Academy of Sciences of the USA* **114**, 2017, E8913–E8921.

Morillon B., Schroeder C.E. and Wyart V., Motor contributions to the temporal precision of auditory attention, *Nature Communications* **5**, 2014, 5255.

Mouraux A. and Iannetti G.D., Across-trial averaging of event-related EEG responses and beyond, *Magnetic Resonance Imaging* **26**, 2008, 1041–1054.

Näätänen R., Paavilainen P., Rinne T. and Alho K., The mismatch negativity (MMN) in basic research of central auditory processing: A review, *Clinical Neurophysiology* **118**, 2007, 2544–2590.

Näätänen R. and Picton T., The N1 wave of the human electric and magnetic response to sound: A review and an analysis of the component structure, *Psychophysiology* **24**, 1987, 375–425.

Nobre A.C., Correa A. and Coull J.T., The hazards of time, *Current Opinion in Neurobiology* **17**, 2007, 465–470.

Pfurtscheller G., Functional brain imaging based on ERD/ERS, *Vision Research* **41**, 2001, 1257–1260.

Pfurtscheller G. and Da Silva F.L., Event-related EEG/MEG synchronization and desynchronization: Basic principles, *Clinical Neurophysiology* **110**, 1999, 1842–1857.

Phillips-Silver J. and Trainor L.J., Feeling the beat: Movement influences infant rhythm perception, *Science* **308**, 2005, 1430–1430.

Polich J., Updating P300: An integrative theory of P3a and P3b, *Clinical Neurophysiology* **118**, 2007, 2128–2148.

van Ede F., Jensen O. and Maris E., Tactile expectation modulates pre-stimulus β-band oscillations in human sensorimotor cortex, *Neuroimage* **51**, 2010, 867–876.

Repp B.H., Sensorimotor synchronization: A review of the tapping literature, *Psychonomic Bulletin and Review* **12**, 2005, 969–992.

Rinne T., Särkkä A., Degerman A., Schröger E. and Alho K., Two separate mechanisms underlie auditory change detection and involuntary control of attention, *Brain Research* **1077**, 2006, 135–143.

Rohenkohl G., Cravo A.M., Wyart V. and Nobre A.C., Temporal expectation improves the quality of sensory information, *Journal of Neuroscience* **32**, 2012, 8424–8428.

Scherg M. and Von Cramon D., Two bilateral sources of the late AEP as identified by a spatio-temporal dipole model, *Electroencephalography and Clinical Neurophysiology* **62**, 1985, 32–44.

Schönwiesner M. and Zatorre R.J., Spectro-temporal modulation transfer function of single voxels in the human auditory cortex measured with high-resolution fMRI, *Proceedings of the National Academy of Sciences of the USA* **106**, 2009, 14611–14616.

Schroeder C.E. and Lakatos P., Low-frequency neuronal oscillations as instruments of sensory selection, *Trends in Neurosciences* **32**, 2009, 9–18.

Schröger E., Giard M.H. and Wolff C., Auditory distraction: Event-related potential and behavioral indices, *Clinical Neurophysiology* **111**, 2000, 1450–1460.

Schröger E., Marzecová A. and SanMiguel I., Attention and prediction in human audition: A lesson from cognitive psychophysiology, *The European Journal of Neuroscience* **41**, 2015, 641–664.

Schubotz R.I., Prediction of external events with our motor system: Towards a new framework, *Trends in Cognitive Science* **11**, 2007, 211–218.

Schubotz R.I., Friederici A.D. and von Cramon D.Y., Time perception and motor timing: A common cortical and subcortical basis revealed by fMRI, *Neuroimage* **11**, 2000, 1–12.

Schubotz R.I. and von Cramon D.Y., Interval and ordinal properties of sequences are associated with distinct premotor areas, *Cerebral Cortex* **11**, 2001, 210–222.

Schubotz R.I. and von Cramon D.Y., Predicting perceptual events activates corresponding motor schemes in lateral premotor cortex: An fMRI study, *Neuroimage* **15**, 2002, 787–796.

Schubotz R.I., von Cramon D.Y. and Lohmann G., Auditory what, where, and when: A sensory somatotopy in lateral premotor cortex, *Neuroimage* **20**, 2003, 173–185.

Sedley W., Gander P.E., Kumar S., Kovach C.K., Oya H., Kawasaki H., et al., Neural signatures of perceptual inference, *Elife* **5**, 2016, e11476.

Snyder J.S. and Large E.W., Gamma-band activity reflects the metric structure of rhythmic tone sequences, *Cognitive Brain Research* **24**, 2005, 117–126.

Spencer K.M., Averaging, detection, and classification of single-trial ERPs, *Event-related Potentials – A Methods Handbook* **209**, 2005.

Spitzer B. and Haegens S., Beyond the status quo: A role for beta oscillations in endogenous content (re) activation, *eNeuro 4 – ENEURO*-0170.2017 2017.

Sridharan D., Levitin D.J., Chafe C.H., Berger J. and Menon V., Neural dynamics of event segmentation in music: Converging evidence for dissociable ventral and dorsal networks, *Neuron* **55**, 2007, 521–532.

Sussman E., Winkler I. and Schröger E., Top-down control over involuntary attention switching in the auditory modality, *Psychonomic Bulletin and Review* **10**, 2003, 630–637.

Teki S. and Griffiths T.D., Working memory for time intervals in auditory rhythmic sequences, *Frontiers in Psychology* **5**, 2014, 1329.

Teki S. and Griffiths T.D., Brain bases of working memory for time intervals in rhythmic sequences, *Frontiers in Neuroscience* **10**, 2016, 239.

Teki S., Grube M., Kumar S. and Griffiths T.D., Distinct neural substrates of duration-based and beat-based auditory timing, *Journal of Neuroscience* **31**, 2011, 3805–3812.

Teki S. and Kononowicz T.W., Commentary: Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery, *Frontiers in Neuroscience* **10**, 2016, 389.

Todorovic A., Schoffelen J.M., Van Ede F., Maris E. and De Lange F.P., Temporal expectation and attention jointly modulate auditory oscillatory activity in the beta band, *Plos One* **10**, 2015, e0120288.

Trainor L.J., Chang A., Cairney J. and Li Y.C., Is auditory perceptual timing a core deficit of developmental coordination disorder?, *Annals of the New York Academy of Sciences* 2018.

Wacongne C., Labyt E., van Wassenhove V., Bekinschtein T., Naccache L. and Dehaene S., Evidence for a hierarchy of predictions and prediction errors in human cortex, *Proceedings of the National Academy of Sciences of the USA* **108**, 2011, 20754–20759.

Wang X.J., Neurophysiological and computational principles of cortical rhythms in cognition, *Physiological Reviews* **90**, 2010, 1195–1268.

Warren J.E., Wise R.J. and Warren J.D., Sounds do-able: Auditory–motor transformations and the posterior temporal plane, *Trends in Neurosciences* **28**, 2005, 636–643.

Wetzel N., Schröger E. and Widmann A., The dissociation between the P3a event-related potential and behavioral distraction, *Physiology* **50**, 2013, 920–930.

Winkler I., Denham S.L. and Nelken I., Modeling the auditory scene: Predictive regularity representations and perceptual objects, *Trends in Cognitive Science* **13**, 2009, 532–540.

Zatorre R.J., Belin P. and Penhune V.B., Structure and function of auditory cortex: Music and speech, *Trends in Cognitive Science* **6**, 2002, 37–46.

Zatorre R.J. and Evans A.C., Lateralization of phonetic and pitch discrimination in speech processing, *Science* **256**, 1992, 846.

Supplementary Materials

Andrew Chang, Dan J. Bosnyak, Laurel J. Trainor

Beta oscillatory power modulation reflects the predictability of pitch change

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S.1 Induced beta power fluctuates at the stimulus presentation rate

We analyzed the beta power on the STD trials in the Predictable sequence, where the same tone was presented isochronously, similarly as in previous studies (Cirelli et al. 2014; Fujioka et al., 2009; 2012; 2015; Iversen et al., 2009). As shown in Figure S1C and D, the beta power desynchonization occurred immediately after the tone onset (0 ms time point), and the power resynchronized prior to the onset time of the next tone at 500 ms point, consistent with previous studies.

We analyzed the time series of each participant's normalized mean induced beta power via short-time Fourier transforms. For each participant, we took the -200 to 700 ms period of the STD trial for the averaged induced beta power (mean power across 15 to 25 Hz) from the wavelet transform, zero-padded to 5 seconds in order to increase the frequency resolution to 0.2 Hz. The amplitude spectrum of the time series of induced beta band power (Figure S1E and F) showed the strongest amplitude at 2.0 Hz (the stimulus repetition rate), and Wilcoxon signed rank tests confirmed this observation that the mean power at 2.0 Hz was significantly larger than the mean power at 1.0, 3.0, 4.0, 5.0 and 6.0 Hz, with all $z > 2.60$ and $p < 0.007$. These results showed that induced beta band power entrains to the presentation rate (2.0 Hz in the present case) of isochronous stimulus sequences.

Although the current study cannot demonstrate beta power entrainment (e.g., Cirelli et al. 2014; Fujioka et al., 2012), due to the lack of variation in stimulus presentation rate and/or use of non-isochronous sequences, the beta power fluctuations observed in the current study are consistent with the pattern of beta power entrainment found in previous studies.

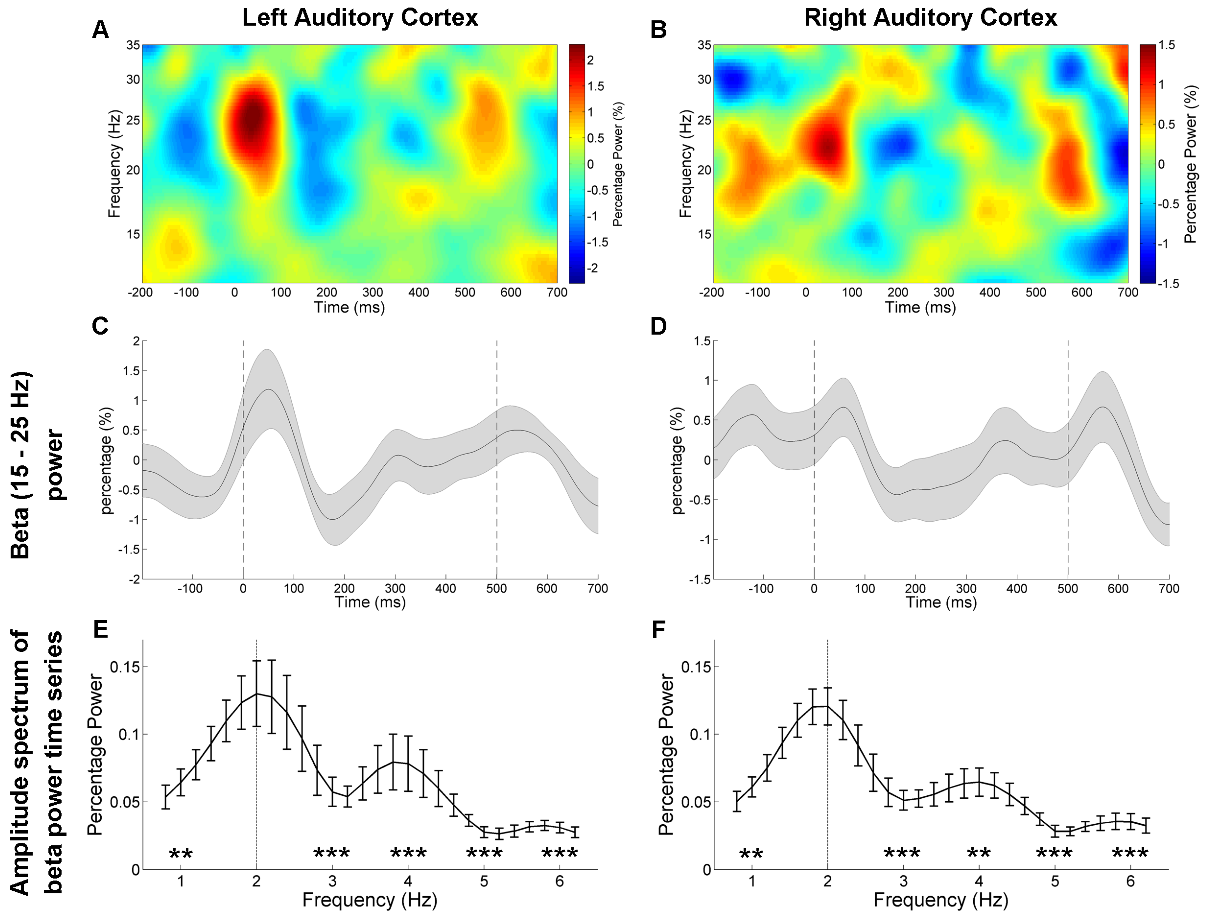

Figure S1. Beta power entrains to the presentation rhythm of tones. The induced (non-phase-locked) oscillatory power was extracted from left (left panel) and right (right panel) auditory cortices using dipole source modeling. (A and B) The time-frequency maps of induced power on STD trials in the Predictable sequence, grand averaged across participants. The onset time of standard pitches are at 0 and 500 ms. (C and D) Beta frequency (15-25 Hz) power was averaged across trials for each participant and is presented as the mean ± standard error across participants. The onset times of standard tones are at 0 and 500 ms. (E and F) The short-time Fourier transform for each beta power time series was averaged across trials for each participant. The amplitude spectrum is shown as the mean ± standard error across participants. Wilcoxon signed rank tests showed that the power at 2.0 Hz (the presentation frequency of the tones) was significantly greater than at 1.0, 3.0, 4.0, 5.0 and 6.0 Hz, showing the induced beta power entrained to the presentation rhythm of auditory tones. ** $p < 0.01$; *** $p < 0.001$.

S.2 Predictability of pitch change and pre-deviant low-beta/high-beta power

Given the effect of predictability of pitch change on pre-deviant beta power, we further explored whether the predictability of pitch change modulates low-beta (15-20 Hz) or high-beta (20-25 Hz) power differently (Figure S2), given that these sub-bands might related to different functions (Kilavik et al., 2013; Spitzer and Haegens, 2017). We quantified the amplitude of desynchronization of the mean low-beta or high-beta power in auditory cortex by measuring the size of the negative peak within the interval of -350 to -150 ms, time-locked to the onset of the deviant pitch.

We examined whether the Predictability of pitch change and high/low beta band have an interaction effect (Figure S2E and S2F). For each participant, we took the desynchronization amplitude difference between Predictable and Unpredictable sequences within low-beta and high-beta band. The Wilcoxon signed rank test did not show a significant effect of the desynchronization amplitude difference between the low-beta and high-beta bands in left auditory cortex ($z = -0.91$, $p = 0.391$) or in right auditory cortex ($z = 1.41$, $p = 0.173$).

Together, this exploratory analysis found that the effect of predictability of pitch change did not differ significantly between the high and low beta bands, suggesting low-beta and high-beta oscillatory activities reflect a similar function in current study.

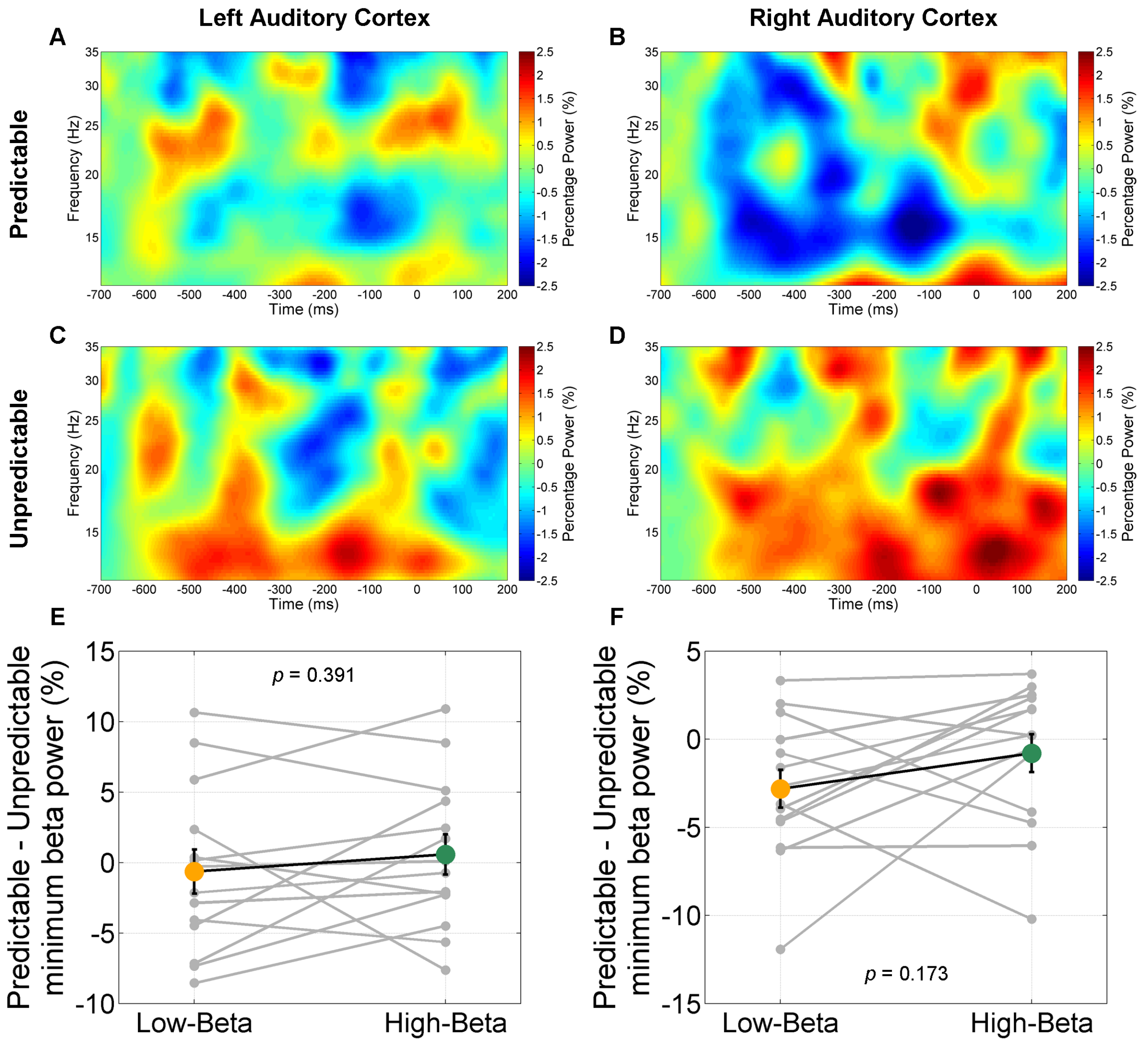

Figure S2. Pre-deviant beta power activities in Predictable and Unpredictable sequences. (A, B, C and D) The time-frequency maps of induced power on preDEV trials in the Predictable and Unpredictable sequences, grand averaged across participants. The onset time of standard pitch is at -500 ms, and the onset time of deviant pitch is at 0 ms. (E and F) The minimum beta power (desynchronization amplitude) in the -350 to -150 ms time window was extracted for each participant for each sequence, and then the difference (Predictable - Unpredictable) was estimated for each participant. The grey dots connected by a grey line represent the data points of each participant, and the colored dots and the error bars represent the conditional mean ± standard error. Wilcoxon signed rank tests did not show any significant effect of high/low beta band interacting with Predictable/Unpredictable sequence on the desynchronization amplitude.

References

Cirelli LK, Bosnyak D, Manning FC, Spinelli C, Marie C, Fujioka T, Ghahremani A, Trainor LJ (2014) Beat-induced fluctuations in auditory cortical beta-band activity: using EEG to measure age-related changes. Front Psychol 5: 742.

Fujioka T, Ross B, Trainor LJ (2015) Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. J Neurosci 35: 15187-15198.

Fujioka T, Trainor LJ, Large EW, Ross B (2009) Beta and gamma rhythms in human auditory cortex during musical beat processing. Ann NY Acad Sci 1169: 89-92.

Fujioka T, Trainor LJ, Large EW, Ross B (2012) Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. J Neurosci 32: 1791-1802.

Iversen JR, Repp BH, Patel AD (2009) Top-down control of rhythm perception modulates early auditory responses. Ann NY Acad Sci 1169: 58-73.

Kilavik BE, Zaepffel M, Brovelli A, MacKay WA, Riehle A (2013) The ups and downs of beta oscillations in sensorimotor cortex. Exp Neurol 245: 15-26.

Spitzer B, Haegens S (2017) Beyond the status quo: A role for beta oscillations in endogenous content (re) activation. eNeuro 4: ENEURO-0170.2017