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Reduced low-frequency power and phase locking reflect restoration in the auditory continuity illusion

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Abstract

Interruptions in auditory input can be perceptually restored if they coincide with a masking sound, resulting in a continuity illusion. Previous studies have shown that this continuity illusion is associated with reduced low-frequency neural oscillations in the auditory cortex. However, the precise contribution of oscillatory amplitude changes and phase alignment to auditory restoration remains unclear. Using electroencephalography, we investigated induced power changes and phase locking in response to 3 Hz amplitude-modulated tones during the interval of an interrupting noise. We experimentally manipulated both the physical continuity of the tone (continuous vs. interrupted) and the masking potential of the noise (notched vs. full). We observed an attenuation of 3 Hz power during continuity illusions in comparison with both continuous tones and veridically perceived interrupted tones. This illusion-related suppression of low-frequency oscillations likely reflects a blurring of auditory object boundaries that supports continuity perception. We further observed increased 3 Hz phase locking during fully masked continuous tones compared with the other conditions. This low-frequency phase alignment may reflect the neural registration of the interrupting noise as a newly appearing object, whereas during continuity illusions, a spectral portion of this noise is delegated to filling the interruption. Taken together, our findings suggest that the suppression of slow cortical oscillations in both the power and phase domains supports perceptual restoration of interruptions in auditory input.

Introduction

Perception of a continuous auditory input stream is remarkably resistant to extraneous disturbances. Under certain circumstances, auditory restoration can occur even for physically discontinuous sounds. For instance, if an ongoing tone is interrupted and this interruption is concurrently masked by broadband noise, individuals typically do not perceive the interruption, but experience a continuity illusion of the tone (Miller & Licklider, 1950). This phenomenon is likely an instance of a more general capacity of the auditory system to maintain stable representations of auditory objects in the presence of interrupting sounds. If the spectral features of the object are expected to remain stable during the interruption, the sounds before, during and after the interruption are perceptually grouped. Illusory continuity breaks down if the noise mask excludes the expected spectrum of the object during the interruption (Warren et al., 1972).

This indicates that the restoration of interrupted auditory objects depends on the potential of the interrupting sound to mask the expected portion of the objects.

The auditory continuity illusion has been described for a wide range of auditory signals, including modulated tones (Ciocca & Bregman, 1987; Kluender & Jenison, 1992; Carlyon et al., 2004; Riecke et al., 2008), music (DeWitt & Samuel, 1990), vowels (Carlyon et al., 2002) and more complex speech stimuli (Warren, 1970). If speech stimuli are used, words are better restored than pseudowords, indicating that besides acoustic similarity, linguistic top-down expectations also modulate the strength of the auditory continuity illusion (Samuel, 1981).

The neuronal mechanisms supporting auditory restoration seem to be organized hierarchically. Recent evidence shows that continuity perception is supported from very early stages in the auditory neural pathway: brainstem responses recorded with electroencephalography (EEG) do not differ between masked interrupted and masked continuous sounds (Bidelman & Patro, 2016). Moreover, single-cell responses to tones in the primary auditory cortex of macaque monkeys are continuous for both interrupting noise and for non-interrupted tones (Petkov et al., 2007). A functional magnetic resonance imaging study (Riecke et al., 2007) has shown that

blood-oxygenation-level-dependent (BOLD) responses in human primary auditory cortex mirror not only basic acoustic stimulus features, but also perceptual groupings of these features. Specifically, BOLD responses to tones were negatively correlated with the masking potential of the interrupting sound when the tone was physically missing during the interruption, that is stronger masking of the tone gap elicited weaker activity. Weaker BOLD responses were consistently observed when participants reported the continuity illusion (vs. veridical discontinuity) given the same acoustic input. For the restoration of more complex speech signals, higher-order and language-relevant areas in both the frontal and auditory cortex are recruited (Heinrich *et al.*, 2008; Shahin *et al.*, 2009; Riecke *et al.*, 2011). Notably, the influence of top-down processing in the auditory continuity illusion is restricted, even for speech-like stimuli: the BOLD activity in the superior and medial temporal gyri, associated with illusory vowel continuity, is not influenced by attention. This indicates that bottom-up processes are sufficient to explain these effects on BOLD activity (Heinrich *et al.*, 2011). Taken together, these results support a neural account of auditory restoration with a prominent contribution of early auditory cortical processing.

Several EEG studies have extended the above-mentioned studies with regard to the underlying temporal neural dynamics, specifically investigating the role of slow oscillatory activity in the auditory continuity illusion (Riecke *et al.*, 2009, 2012; Shahin *et al.*, 2012). A study using noise-interrupted amplitude-modulated tones found increased 4 Hz power approximately 150 ms after the onset of interruptions, compared with physically uninterrupted stimuli (Riecke *et al.*, 2009). However, this power increase was reduced when interruptions were fully masked. Importantly, the theta power increase was also reduced when participants perceived a continuity illusion vs. when they perceived an interruption. In other words, theta oscillations appeared to be suppressed when auditory restoration occurred compared to when it did not occur, despite identical sensory input. This pattern roughly matches that observed for the BOLD responses described above (Riecke *et al.*, 2007). The authors suggested that differences in phase locking could underlie the observed modulations, but no direct analysis of phase-related measures was performed in that study.

The above-described findings are compatible with a more general role of low-frequency oscillations for attention-driven temporal segmentation of incoming auditory signals. In this framework, phase locking of neural oscillations to intensity modulations of the input stream enables the alignment of periods of high neural excitability to the expected arrival time of auditory events (Schroeder & Lakatos, 2009). Another study, using interrupted words, found restoration-related effects on inter-trial coherence (ITC) in the 4–8 Hz range, and auditory evoked potential amplitudes, with higher ITC, N1 and P2 amplitudes for perceived interruptions compared to continuity illusions (Shahin *et al.*, 2012).

In summary, low-frequency oscillations appear to play a major role in the formation of the continuity illusion and auditory objects, but the relative contributions of phase locking and power increases remain unclear.

In this study, we aimed to further elucidate the relationship between low-frequency EEG oscillations and the continuity illusion. More specifically, we aimed at replicating the previously observed stimulus-related modulations of low-frequency oscillations (Riecke *et al.*, 2009, 2012) and extending these findings by clarifying whether these modulations can be attributed to the induction of oscillatory amplitude changes, the phase alignment of ongoing oscillations, or both. To do so, we analysed induced power changes and ITC for various levels of sound continuity and masking, in an auditory continuity judgement task.

Materials and methods

Participants

Twenty-three healthy participants were recruited from the general population. All participants had normal hearing (< 25 dB hearing level) and normal or corrected to normal vision and no record of neurological or psychiatric disorders. Three participants were excluded because they gave invariant behavioural responses across conditions (see "Analysis of behavioural data"). Moreover, three participants were excluded due to insufficient quality of their EEG data. The mean age of the remaining 17 participants (six female, 15 right-handed) was 36 years (range: 24–50 years). The experimental procedures were conducted in accordance with the declaration of Helsinki and approved by the ethics committee of the Charité – Universitätsmedizin Berlin. Prior to the experiment, each participant gave written informed consent.

Stimuli and design

Auditory stimuli were presented from a central speaker below a CRT monitor, and the stimulus intensity was set to 70 dB sound pressure level. During the experiment, a central, dark gray fixation cross was presented on a gray background, which had a luminance of 21 cd/m^2.

Auditory stimuli had duration of 2.8 s and were sampled at 44 100 Hz. They consisted of 930 Hz pure tones, which were amplitude-modulated at 3 Hz (sinusoidal modulation, depth: 100%, fixed phase), and a noise burst (mask). The tone was either continuous or interrupted with a central 0.6-s silent period. The mask consisted of white noise that was bandpass-filtered into a 2-octave region centred on the tone frequency. The mask started 1.1 s after tone onset, so that it overlapped with the central 0.6 s of the tone. Tone and mask onsets and offsets were linearly ramped with 3 ms rise-fall times, with ramp centres of the mask synchronized with those of the adjoining tones (for further details, see Riecke *et al.*, 2009). The masking potential of the noise was varied by either bandstop-filtering it in the 0.6-octave range centred on the tone frequency (notched mask), or leaving the noise unchanged (full mask). Hence, the study comprised a 2 × 2 factorial design with the factors Tone Continuity (continuous vs. interrupted) and Masking Level (notched vs. full). We refer to the four stimulus types as continuous tone and full mask (CF); continuous tone and notched mask (CN); interrupted tone and full mask (IF); and interrupted tone and notched mask (IN; Fig. 1).

For each of the four stimulus types, 120 trials were presented. These 480 trials were presented across 12 blocks, during which the four stimulus types were randomly intermixed. Participants were asked to rate the continuity of the tone on a scale from 1 (very likely interrupted) to 4 (very likely continuous) by pressing a button with the index finger of the right hand after each trial. The response window started 0.8–1.2 s after tone offset, had duration of 0.5 s and was indicated by a red fixation cross. Participants did not receive feedback. The inter-trial-interval varied randomly from 2 to 2.5 s, resulting in total trial duration of 6.1–7 s. The total duration of the experiment including breaks, but excluding EEG preparation, was approximately 80 min.
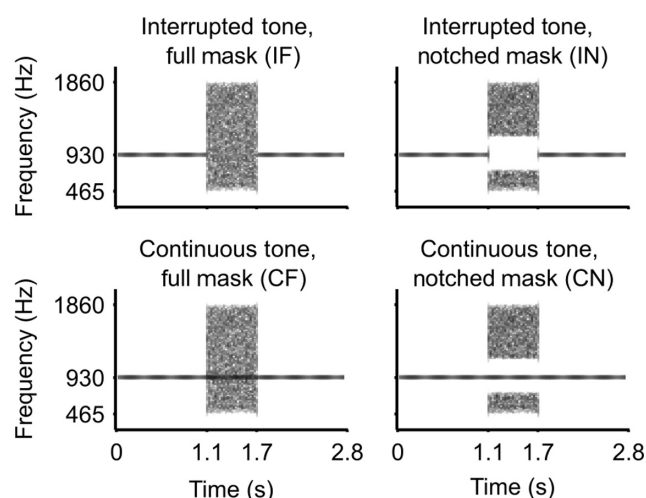
FIG. 1. Schematic spectrograms of the four stimulus types. Stronger signal intensity is indicated by darker colours.

Analysis of behavioural data

Behavioural performance was assessed using a one-way ANOVA with factor Stimulus Type separately for each participant to determine whether the participant could differentiate the four stimulus types. Three subjects who gave invariant responses ($P > 0.05$) were removed from further analysis. In the next step of the analysis, a two-factorial ANOVA across subjects with the factors Tone Continuity and Masking Level was performed. Significant behavioural effects were followed up using *post hoc* t-tests with Holm-correction for multiple testing.

Acquisition and preprocessing of EEG data

Electroencephalography was recorded using an active 128-electrode cap (EasyCap, Herrsching, Germany), including two electrooculography electrodes placed below and lateral to the right eye to monitor eye movements, and Brainamp DC amplifiers (Brainproducts, Gilching, Germany). Data were recorded in reference to an electrode positioned on the nose at a sampling frequency of 1000 Hz, with an online 0.1 Hz high-pass filter and a 250 Hz low-pass filter.

Electroencephalography data processing was performed in MATLAB (MathWorks, Natick, MA, USA) using the EEGLAB (Delorme & Makeig, 2004) and FIELDTRIP (Oostenveld *et al.*, 2010) toolboxes and custom scripts. Data were first high-pass filtered at 1 Hz and then low-pass filtered at 150 Hz. The default EEGLAB filter settings were applied, resulting in a one-pass non-causal zero-phase Hamming-windowed sinc FIR filter, with a filter order of 3300 and a −6 dB cut-off frequency of 0.5 Hz for the high-pass, and a filter order of 88 and a cut-off frequency of 168.75 Hz for the low-pass filter. High-pass filtering with these settings is expected to have only minor effects on early evoked components (Widmann *et al.*, 2015). Line noise was removed by fitting a 50 Hz sinusoid signal in segments of 4 s and subtracting the fitted signal from the data (*cleanline* plugin in EEGLAB). Data were subsequently downsampled to 500 Hz and epoched from −1 to 2.8 s relative to auditory stimulus onset. Trials and channels that contained large artefacts were removed following visual inspection. Then, data were re-referenced to common average and subjected to independent component analysis using the extended infomax algorithm as implemented in EEGLAB (*runica,* see Lee *et al.*, 1999). Components that represented eye

blinks, cardiac or muscle activity were removed. Afterwards, the electrooculography channels were removed from the data, and rejected EEG channels were interpolated using spherical interpolation. Trials that still exceeded a threshold of ±150 μV after these procedures were rejected. On average, 43.9 (±25.7 SD) trials, 6.4 (±3.5 SD) channels and 10 (±2.9 SD) components were removed from each dataset. A one-way repeated measures ANOVA indicated no differences in final trial count between conditions across participants ($F_{3,16} = 0.59$, $P = 0.6216$). Descriptive statistics of trial counts are shown in Table 1.

Analysis of induced oscillations

For the analysis of induced neural oscillations, first the condition-specific average waveforms (i.e. event-related potentials) were subtracted from the single-trial time series to reduce phase-locked activity. The resulting data were time-frequency transformed using a single Hanning window with a frequency-dependent window length (3 cycles/frequency) at a resolution of 1 Hz. Time-frequency analysis was performed for the interval from −0.8 to 2.4 s in 25-ms steps. Then, the time-frequency representation was normalized relative to baseline (the 0.5-s interval prior to noise onset, i.e. 0.6–1.1 s after auditory stimulus onset) using decibel conversion. Following the approach of Riecke *et al.* (2009), we focused the analysis on average power at mediocentral electrodes in the time range of 0.1–0.4 s after noise onset in the 3–7 Hz frequency range.

Electroencephalography power was analysed using the same statistical model as the behavioural data, that is a repeated measures ANOVA with the factors Tone Continuity (continuous vs. interrupted) and Masking Level (notched vs. full), separately for each frequency. The statistical outcome of the ANOVA was Holm-corrected for multiple comparisons in the five frequency bins.

Analysis of phase consistency

We analysed inter-trial coherence to directly investigate the contribution of phase consistency across trials to the previously observed power effects. ITC was calculated from the preprocessed data without prior subtraction of the event-related potentials, using the same parameters for the time-frequency transformation as for the analysis of induced power. ITC was computed by unit-normalizing the amplitude information of the spectral activity in each trial, averaging the complex values across trials and calculating the modulus. The resulting value indicates the amount of phase synchronization across trials (Tallon-Baudry *et al.*, 1996). Analogously to the analysis of behaviour and power, log-transformed ITC values at frequencies revealing significant changes were submitted to a two-way ANOVA with the factors Tone Continuity and Masking Level.

Supplemental analyses

To rule out that spurious phase-locked activity underlie the observed effects on induced power, we computed event-related potentials for all stimulus conditions, applying a 30 Hz low-pass filter (sixth-order Butterworth, two-pass) and baseline correction with the 200-ms interval prior to noise onset. We computed N100 and P200 peaks as the minima/maxima of the averaged responses over subjects from 0 to 0.2 s and 0.1 to 0.3 s after noise onset, respectively. We then averaged the individual responses over a 30-ms time window around the peak latency and again submitted the data to a two-way ANOVA. To rule out that power differences affected the computation of ITC, we also analysed differences in raw power

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(without subtraction of the event-related response, without baseline correction). Again, a two-way ANOVA was used to evaluate the differences.

Results

Behavioural

Listeners reported IF tones on average as continuous, whereas they reported IN tones veridically as discontinuous, as was expected. Statistical analysis of perceived continuity revealed main effects for Tone Continuity ($F_{1,16} = 456.52$, $P < 0.001$) and Masking Level ($F_{1,16} = 195.6$, $P < 0.001$). In addition, an interaction between the two factors was found ($F_{1,16} = 277.27$, $P < 0.001$). Follow-up t-tests showed that continuity ratings were higher for CF compared to IF tones ($t = 3.53$, $P = 0.0055$), for IF compared to IN ($t = 15.6$; $P < 0.001$) as well as for CN compared to IN tones ($t = 25.81$, $P < 0.001$, Fig. 2A). Taken together, these behavioural results indicate that interrupted tones induced continuity illusions only when their gap was masked, consistent with the results of previous studies.

Induced oscillations

The ANOVA of induced power revealed a main effect for Masking Level at 3 Hz ($F_{1,16} = 8.79$, $P = 0.0456$). Furthermore, an interaction between Tone Continuity and Masking Level was obtained at 3 and 6 Hz ($F_{1,16} = 11.63$, $P = 0.0179$ and $F_{1,16} = 10$, $P = 0.0241$, respectively). Using a shifted baseline window from 0.5 to 1 s after stimulus onset yielded a similar outcome. Follow-up t-tests with Holm-correction showed that 3 Hz power was

higher for the IN tone compared to the IF tone ($t = 4.28$, $P = 0.0023$) and higher for the CF tone compared to the IF tone ($t = 2.9$, $P = 0.0318$, Fig. 2B). Three Hz power was increased in all conditions compared to baseline. Follow-up tests for the 6 Hz frequency bin resulted in no significant effects. The consistent, but smaller interaction for 6 Hz power may reflect co-entrainment at the second harmonic of the tone modulation frequency (Ross *et al.*, 2000; Ali *et al.*, 2013).

Phase consistency

For the ITC at 3 Hz, no main effect was found (*P*-values > 0.05). However, the ANOVA revealed a significant interaction between Tone Continuity and Masking Level ($F_{1,16} = 8.01$, $P = 0.0121$). Follow-up tests revealed that the 3 Hz ITC was higher for CF compared to IF tones ($t = 3.77$, $P = 0.0061$), thus matching the 3 Hz power results above. Furthermore, 3 Hz ITC was higher for CF compared to CN tones ($t = 3.81$, $P = 0.0061$, Fig. 2C).

Supplemental analyses

The supplemental analysis of event-related potentials revealed a main effect of Masking Level on N100 and P 200 amplitudes ($F_{1,16} = 7.2$, $P = 0.0163$ and $F_{1,16} = 8.53$, $P = 0.01$, respectively). No significant interaction effects on N100 and P200 amplitudes were found ($F_{1,16} = 3.45$, $P = 0.0818$ and $F_{1,16} = 0.26$, $P = 0.6153$, respectively). N100 amplitudes were on average more negative in the notched mask conditions, while P200 amplitudes were more positive in the fully masked conditions. Event-related potentials are shown in Fig. 3.

TABLE 1. Mean and SD for trial count, behavioural rating, 3 Hz power, ITC, N100 and P200 amplitudes in each condition. Larger values of behavioural ratings represent stronger continuity percepts

	Trial count	Behavioural rating	Power change (dB)	log ITC	N100 amplitude (µV)	P200 amplitude (µV)
CF	95 ± 9.89	3.65 ± 0.3	0.93 ± 0.91	−1.11 ± 0.39	−1.02 ± 0.95	2.41 ± 1.04
CN	95.65 ± 8.53	3.7 ± 0.29	0.83 ± 0.86	−1.25 ± 0.49	−1.14 ± 0.78	1.97 ± 1.15
IF	95.88 ± 10.34	3.34 ± 0.57	0.5 ± 0.74	−1.28 ± 0.41	−0.73 ± 0.9	2.39 ± 1.20
IN	94.29 ± 11.43	1.28 ± 0.27	1.13 ± 0.83	−1.19 ± 0.52	−1.2 ± 0.77	2.15 ± 1.21

CF, continuous tone and full mask; CN, continuous tone and notched mask; IF, interrupted tone and full mask; IN, interrupted tone and notched mask; ITC, inter-trial coherence.
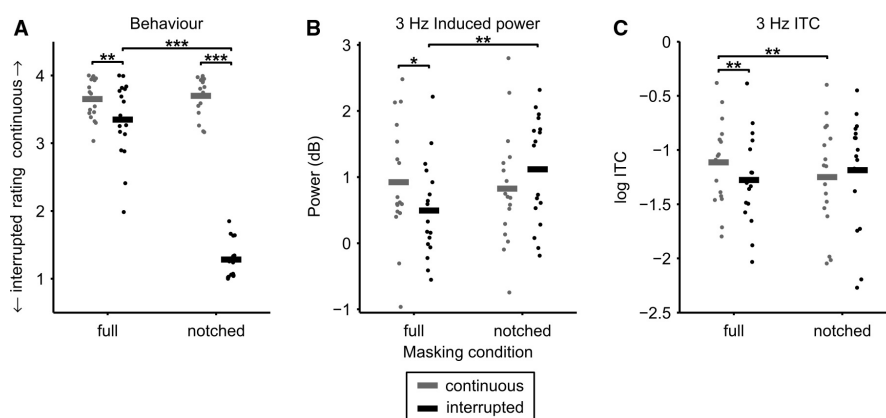

FIG. 2. Left panel (A): Mean behavioural ratings, indicated by bars, and individual ratings, indicated by dots. Significant results from follow-up tests are indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Middle panel (B): same as A, but for induced 3 Hz power changes. Right panel (C): same as A and B, but for log-transformed inter-trial coherence at 3 Hz.

For non-baseline-corrected 3 Hz power, we found an interaction effect ($F_{1,16}$ = 14.03, P = 0.0018). *Post hoc* tests showed that power was higher for IN compared to CN tones (t = 3.11, P = 0.0266), while the other comparisons did not reach significance (IF-CF: t = −2.5, P = 0.0678; IN-IF: t = 2.04, P = 0.0678; CN-CF: t = −2.43, P = 0.0678). We also tested for raw power differences in the baseline window and found no main or interaction effects (P > 0.05).

Descriptive statistics of behavioural ratings, 3 Hz power, ITC and N100 and P200 amplitudes are shown in Table 1. Spectrograms and topographic distributions of power and ITC are shown in Fig. 4.

Discussion

In this study, we examined the role of induced and phase-locked oscillations for the auditory continuity illusion, using an analysis of perceived continuity ratings, induced power changes and phase locking across trials. On the behavioural level, we found clearly decreased continuity ratings in the IN condition, where the interruption is detected due to partial unmasking and relatively high ratings in the IF condition, where the interruption is perceptually restored due to full masking. These behavioural effects are paralleled by modulations of induced 3 Hz oscillations, with enhanced power for gap detection and attenuated power for the continuity illusion. Phase locking was selectively increased in the CF condition, where a continuous tone and a full mask coincide.

We found an interaction effect on continuity ratings, which was mainly driven by low continuity ratings in the IN condition and, conversely, high continuity ratings in the IF condition. Continuity ratings were also slightly lower in the IF condition compared to the CF condition, but still much higher than for IN stimuli. In other words, continuity ratings reflected the detection of a gap in the tone in the IN condition and continuity illusions in the IF condition. Ratings in the continuous conditions were high, in accord with predictions. Thus, our behavioural results replicate previous findings (Warren, 1970; Riecke *et al.*, 2008) and show that our IF stimuli successfully elicited continuity illusions.

In the analysis of oscillatory activity during the interval of the interruption, we found an increase in induced 3 Hz power in all conditions compared to the pre-interruption interval, which

FIG. 3. Event-related potentials for the four stimulus conditions. Noise on- and offsets are indicated by vertical dotted lines, and the time windows for peak detection are indicated by red lines below/above the respective potentials.

contained only the tone. This is in line with previous reports (Riecke *et al.*, 2009). We also found that the power increase was further enhanced by removing the tone frequency and nearby frequencies from the mask (notched vs. full mask). In addition to this main effect of Masking Level, we found an interaction between Masking Level and Tone Continuity: the power increase was attenuated for interrupted, fully masked (IF) stimuli, but it was enhanced for interrupted, partially masked (IN) stimuli. Importantly, IF stimuli were perceived as continuous, whereas IN stimuli were perceived as interrupted. This pattern, with a reduction in power for continuity illusions and an increase in power for gap detection, is broadly consistent with the findings of Riecke *et al.* (2009). Interestingly, our results differ with regard to the power modulations by physical Tone Continuity: while Riecke *et al.* (2009) found overall lower theta power for continuous compared to interrupted stimuli, we could not replicate this main effect of Tone Continuity. By contrast, our data show that 3 Hz power increases in the physically continuous conditions attain intermediate levels, which may reflect the encoding of a change in the auditory scene induced by the onset of the overlaid mask. There are some notable differences between the current experiment and the study by Riecke *et al.* (2009) that could explain the relatively high power in the physically continuous conditions and, consequently, the absence of a main effect for Tone Continuity. In the current experiment, data were not reconstructed from specific independent components thought to reflect auditory processing, but the full-dimensional signal at electrodes of interest was analysed. Furthermore, we conducted ANOVA not on averaged theta (3–7 Hz) power, but for each frequency separately. This analysis with higher resolution in the frequency domain may have exposed power increases in the continuous conditions that were possibly blurred over frequencies in the previous study. In summary, differences in the analysis strategies may account for differences in the effect of physical Tone Continuity. Critically, the analysis of evoked potentials yielded only a main effect of Masking Level, but no interaction effect. This difference in effect patterns indicates that the induced power changes are not driven by spurious evoked activity.

Studies using related auditory illusion paradigms have obtained similar results (Leske *et al.*, 2014; Müller *et al.*, 2013). For example, in an auditory illusion paradigm using noise-masked music, Müller *et al.* (2013) found that the illusory restoration of familiar music during noise is associated with reduced low-frequency power in the auditory cortices. Furthermore, Leske *et al.* (2014) found that the strength of an auditory illusion and the reduction in low-frequency power were related to the level of the masking noise. Hence, our results replicate previous findings and corroborate the idea that the restoration or filling in of a temporal auditory gap is associated with the attenuation of low-frequency oscillations. In contrast, an enhancement of power can be observed if auditory interruptions are unmasked and therefore detected. Recent EEG research in auditory continuity has also focused on higher-frequency bands: prestimulus power in the gamma band was found to predict illusory perception, with higher power before stimulus onset linked to stronger continuity illusions (Vinnik *et al.*, 2012). This study used a 40 Hz amplitude-modulated sound, which elicited a steady-state response at the AM frequency. However, the response did not persist during noise, when participants perceived a continuity illusion. It is notable that the modulations of oscillatory power that were related to auditory restoration were observed at the tone AM frequency in our study as well as in previous studies.

To extend the analysis of induced power, we investigated stimulus-related changes in phase locking. We found that ITC at 3 Hz was selectively increased in the CF condition relative to other
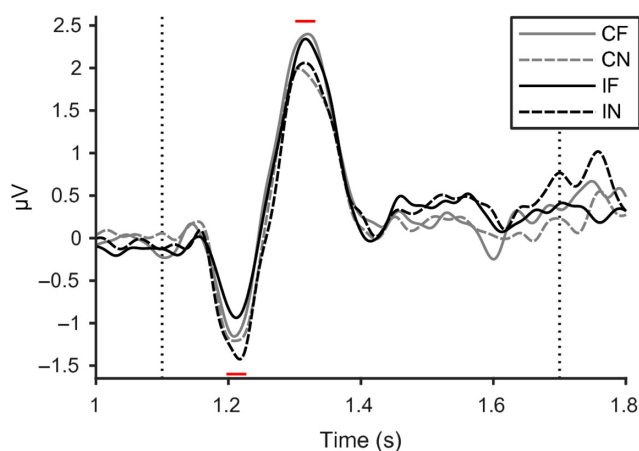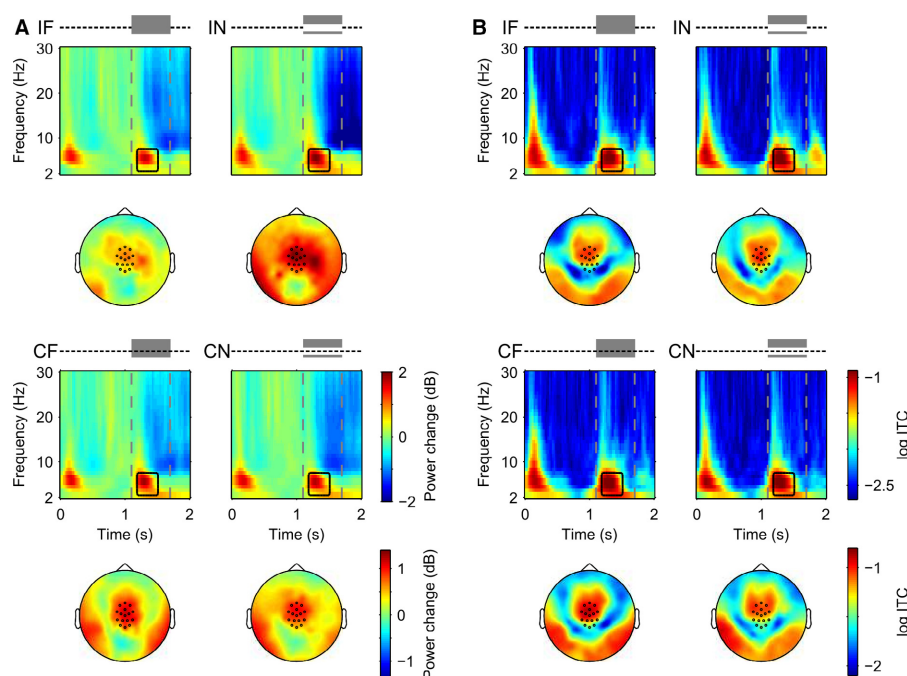
FIG. 4. Left panel (A), top rows: Spectrograms of induced power changes for all conditions. Noise mask on- and offset are indicated by dashed lines, and schematic stimuli are displayed above the spectrograms. The analysed time-frequency window is indicated by the black box. Bottom rows: Topographic distributions of 3 Hz induced power change within the time window of interest. Analysed channels are indicated by circles. Right panel (B): same as A, but for log-transformed ITC values.

conditions. Note that no such effect was observed in the analyses of power and that ITC did not merely follow the pattern of evoked responses. This shows that the superposition of an amplitude-modulated continuous tone and a spectrally overlapping noise mask leads to increased low-frequency phase locking at the onset of the mask. The increase in phase locking in the CF condition may reflect the registration of the mask as a newly appearing object, whereas in the IF condition, listeners illusorily attributed a spectral portion of this mask to the interrupted tone, thus likely reducing both the perceived level of the mask (McAdams *et al.*, 1998) and the phase locking elicited by it. Importantly, the relatively high power in the IN and CN conditions was not associated with phase alignment; thus, it must have originated from an amplitude increase in ongoing oscillations. Our ITC results differ from the findings of Shahin *et al.* (2012), who observed increased phase locking in the 4–8 Hz range for interrupted compared to continuous words masked by noise. This association of gap detection and phase locking may be due to a greater reliance on phase information in speech processing, as suggested by findings from various studies of cortical speech tracking (Peelle & Davis, 2012). With respect to the relationship between power and ITC, Riecke *et al.* (2009) hypothesized that increased theta power for gap detection 'could reflect spontaneous attention-related phase-locking of slow ongoing neuronal oscillations to the target's AM which enhanced the salience of gaps' (p. 556). Our findings did not corroborate this hypothesis, as phase locking was not significantly increased for IN compared to IF stimuli – that is, for gap detection vs. continuity illusion. Instead, our results suggest that phase locking is increased particularly when the amplitude-modulated tone and the full noise mask coincide. With respect to the role of ITC for the auditory restoration, Riecke *et al.* (2009) argued that 'restoration of an interrupted sound depends on the suppression of neuronal phase-locking to that sound's acoustic structure' (p. 556). The current results tentatively support this hypothesis, because we found

relatively low ITC but also attenuated power during the perception of the auditory continuity illusion. Importantly, raw power was selectively increased in the IN compared to the CN condition, but no significant differences between the CF and any other condition were found. This suggests that the increased ITC in the CF condition is not attributable to elevated raw power.

To summarize our key findings with regard to power and phase, induced power at 3 Hz during the noise mask is attenuated when interruptions are fully masked and perceptually restored, but enhanced when interruptions are partially unmasked and perceptually detected. This suggests that the suppression of low-frequency oscillations is related to the blurring of auditory boundaries. Phase locking increases when continuous tones and full noise masks are overlaid, which may reflect the emergence of a new object in the auditory scene. In comparison with Riecke *et al.* (2009), power in the CF condition was higher, which was paralleled by increased phase locking in this condition. Apparently, the stimulus consisting of continuous tone and full mask induced not only an increase in oscillatory amplitude, but also a phase alignment of the oscillation, whereas this phase alignment was largely absent for other conditions.

Auditory perception depends on both the power and phase of entrained low-frequency oscillations. Ng *et al.* (2012) showed that missed targets embedded in noise are preceded by increased theta power and phase locking. This result demonstrates that, while entrainment can generally be beneficial during attentive processing, it can also impair stimulus detection in noisy environments and underlines the complex interplay of oscillations and perceptual accuracy. Florin *et al.* (2017) recently demonstrated that theta and beta power modulations prior to stimulus onset could predict successful pitch discrimination. While the experimental logic in these studies differs from ours in the sense that perceptual accuracy cannot easily be related to illusory restoration, the results nevertheless affirm the relevance of low-frequency oscillations in auditory perception.

Oscillatory phase alone has been shown to modulate auditory perceptual accuracy, with a benefit for gap detection at certain phases of entrained oscillations (Henry & Obleser, 2012). The ability to detect gaps in 3 Hz frequency-modulated sound depended on the phase of stimulus modulation and entrained delta oscillations, with neural delta phase predicting performance better than stimulus phase. The authors postulate that modulated stimuli phase reset and entrain neural oscillations, which then modulate the excitation/inhibition cycle, and consequently detection rates. As gaps always occurred at a fixed phase in our stimulus set, we were restricted to analysing the effect of stimulus properties on phase locking. In addition to the reported effects of power on restoration, it would be interesting to directly test the effect of phase in a modified continuity illusion paradigm where masked gaps are distributed uniformly around the AM frequency cycle. This approach could reveal phase-related changes in auditory restoration that are not reflected in stimulus-related ITC differences.

Conclusion

In the current experiment, we explored the neural mechanisms underlying the auditory continuity illusion. We successfully replicated the perception of the continuity illusion and the associated attenuation of neural low-frequency oscillatory power. Importantly, we extended previous findings and suggest a dual role of low-frequency power in auditory perception: reduced low-frequency power could be related to the restoration of an interrupted sound, whereas increased low-frequency power is likely related to the detection of auditory boundaries. Our study also revealed increased phase locking during the perception of continuous tones overlaid with a full noise mask. Thus, increased phase locking may indicate the encoding of an additional object in the auditory scene. Taken together, our results highlight the interplay between restoration, gap detection and auditory scene analysis and the potential mediating role of low-frequency oscillations in these processes.

Acknowledgements

Conflict of interest

The authors declare the absence of any relationships that could be construed as a potential source of conflict of interest.

Data accessibility

The raw study data cannot be made available because participants did not consent to public dissemination. Processed data and analysis scripts can be made available upon request.

Author contributions

MK analysed the data and drafted the manuscript, YRR acquired and analysed the data, LR and DS conceived the experiment and critically revised the manuscript, and JK analysed data and critically revised the manuscript.

Abbreviations

BOLD, blood-oxygenation-level-dependent; EEG, electroencephalography; ITC, inter-trial coherence.

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