

ORIGINAL ARTICLE

Within- and between-subject consistency of perceptual segmentation in periodic noise: A combined behavioral tapping and EEG study

Hanna Ringer^{1,2}  | Erich Schröger²  | Sabine Grimm^{2,3} 

¹International Max Planck Research School NeuroCom, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

²Wilhelm Wundt Institute for Psychology, Leipzig University, Leipzig, Germany

³Institute of Physics, Chemnitz University of Technology, Chemnitz, Germany

Correspondence

Hanna Ringer, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany.
Email: hringer@cbs.mpg.de

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: GR3412/2-2

Abstract

It is remarkable that human listeners can perceive periodicity in noise, as the isochronous repetition of a particular noise segment is not accompanied by salient physical cues in the acoustic signal. Previous research suggested that listeners rely on short temporally local and idiosyncratic features to perceptually segment periodic noise sequences. The present study sought to test this assumption by disentangling consistency of perceptual segmentation within and between listeners. Presented periodic noise sequences either consisted of seamless repetitions of a 500-ms segment or of repetitions of a 200-ms segment that were interleaved with 300-ms portions of random noise. Both within- and between-subject consistency was stronger for interleaved (compared with seamless) periodic sequences. The increased consistency likely resulted from reduced temporal jitter of potential features used for perceptual segmentation when the recurring segment was shorter and occurred interleaved with random noise. These results support the notion that perceptual segmentation of periodic noise relies on subtle temporally local features. However, the finding that some specific noise sequences were segmented more consistently across listeners than others challenges the assumption that the features are necessarily idiosyncratic. Instead, in some specific noise samples, a preference for certain spectral features is shared between individuals.

KEYWORDS

auditory processes, EEG, oscillation/time frequency analyses, sensation/perception

1 | INTRODUCTION

The human auditory system is remarkably sensitive in perceiving repeating patterns in acoustic input (for a recent review, see Chait, 2020). In fact, the sensitivity to complex acoustic patterns in rapid tone sequences has been found to be comparable with that of an ideal observer, and does

not even require attention (Barascud et al., 2016). Efficient perception and memory of spectrotemporal dynamics (i.e., changes in the frequency spectrum over time) play an essential role to understand and successfully interact with the environment because auditory information, by its very nature, only carries meaning as a sequence unfolding in time (Chait, 2020; Maravall et al., 2018). Especially

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Psychophysiology* published by Wiley Periodicals LLC on behalf of Society for Psychophysiological Research.

(spectro-) temporal regularities act as a particularly useful cue during auditory scene analysis, enabling identification and segregation of sound sources, the temporal segmentation of a continuous signal, prediction of future events and detection of changes in the environment, thereby facilitating higher-level cognitive processes and planning of adaptive behavioral reactions (Bendixen, 2014; Bregman, 1990; Nelken et al., 2014; Winkler et al., 2009).

The present study focuses on how periodic recurrences of complex acoustic patterns embedded in a continuous sound signal enable temporal segmentation of the sound stream. In particular, we are interested in within-listener and between-listener consistency of temporal segmentation of random auditory waveforms (i.e., noise). For this type of stimulus material, temporal segmentation needs to be mainly guided by the memory-based detection of recurrences of spectrotemporal patterns because the sound signal itself does not contain a limited number of salient features, but a multitude of only subtle acoustic cues that could be used for bottom-up driven segmentation.

1.1 | Periodicity detection in acoustic noise

Remarkably, recurring patterns can even be detected in acoustic material that is otherwise largely unstructured, such as white noise. Physically speaking, white noise is a random signal generated from a series of uncorrelated samples, which results in a flat power spectrum. It is perceived as a homogeneous sound texture devoid of outstanding characteristic features (such as pitch or envelope modulations) that would make it easy to distinguish different specific noise tokens or detect repetitions of a specific segment within a noise sequence (Kaernbach, 2004). Listeners were found to be able to behaviorally recognize periodicity in noise without prior training (Guttman & Julesz, 1963) and tap consistently to the perceived structure in periodic noise across presentations of the same noise sequence (Kaernbach, 1992, 1993; Limbert & Patterson, 1982). However, several studies observed differences in tapping consistency between different subjects and between different noise samples (Kaernbach, 1992, 1993; Limbert & Patterson, 1982). The authors attributed these differences to the virtually infinite number of perceptual features within a noise sample that may become salient after periodically repeated exposure and are perceived as “clanks” or “rasping” (Kaernbach, 1992, 1993; Limbert & Patterson, 1982). Although it has been proposed that representations of complex acoustic input generally rely on statistical sound information that is averaged over time (thereby reducing required storage capacity and temporal detail), repeated presentation might enable the retention

of temporally local details that would not be retained when hearing the stimulus only once (McDermott et al., 2013).

Detection of periodicity in noise sequences is also reflected in characteristic electrophysiological responses. In the first studies, naïve listeners were presented with (interleaved) periodic noise sequences, that is, short noise segments recurring isochronously, alternated with portions of random noise between the repetitions. They found an early frontocentral negativity that was time-locked to the onset of the repeating segment, and its magnitude was positively correlated with participants' performance in detecting disruptions in the periodicity (Kaernbach et al., 1998). Notably, the onset of the repeating noise segment elicited a negativity irrespective of whether or not listeners attended to the auditory stimulation (Berti et al., 2000). It was associated with automatic memory-related processes, tuning the auditory system to enhance its perceptual sensitivity to subtle features in the recurring noise segment (Kaernbach et al., 1998).

1.2 | Perceptual learning of periodic white noise

The ability to detect temporal regularities and make use of them to structure incoming auditory information depends on memory representations for repeating acoustic patterns.

Although the recognition memory is generally deemed to be inferior in the auditory compared with the visual domain (Cohen et al., 2009), there is compelling evidence that the human brain is exceptionally capable of rapidly forming robust short- and longer-term memories for various types of random auditory patterns, such as tone pip sequences (Bianco et al., 2020), temporal patterns of clicks (Kang et al., 2017), and white noise (Agus et al., 2010). It has been argued that listeners build up these representations during perceptual learning, which refers to experience-dependent changes in the perceptual ability to effectively extract and use information from sensory input through repeated exposure (Gibson, 1969; Gilbert et al., 2001).

Several studies have shown the formation of robust auditory memories for (seamless) periodic noise (Agus et al., 2010; Agus & Pressnitzer, 2013; Viswanathan et al., 2016). In a periodicity detection task, hit rate gradually increased for periodic noises that were, unbeknownst to the participants, repeated over the course of the experiment, indicating that listeners learned these noises through repeated exposure (Agus et al., 2010). Apart from happening implicitly and automatically, learning occurred fast and memory representations were characterized as resilient to interference from task-irrelevant noises, robust against temporal and spectral transformations, and

long-lasting (Agus et al., 2010; Viswanathan et al., 2016). Interestingly, noise samples differed in terms of learning success, such that some of them were learned almost perfectly, while others were not learned at all. These differences could not be attributed to systematic variation neither between listeners nor between specific noise samples. Therefore, the authors suggested that perceptual learning relies on short temporally local features, which are (at least partly) idiosyncratic, that is, specific to listeners and noise samples (Agus et al., 2010).

The observed increase in perceptual sensitivity was proposed to be achieved via resetting the phase of ongoing low-frequency neural oscillations to these features (Luo et al., 2013), thereby aligning sensitivity fluctuations to time windows when critical events are most likely to occur (Henry & Obleser, 2012). Concretely, inter-trial phase coherence (ITPC) of low-frequency oscillations (2–8 Hz) became gradually stronger for periodic noises that were presented repeatedly over the course of the experiment (Luo et al., 2013). Notably, different noise patterns elicited distinguishable neural phase patterns (Luo et al., 2013). This finding later found support from an fMRI study that demonstrated distinguishable activation patterns in planum temporale and hippocampus for previously implicitly learned noise-like patterns (Kumar et al., 2014). ITPC in the frequency of the stimulation was also enhanced for regularly repeating patterns in sequences of short tones and narrow-band noises (Herrmann & Johnsrude, 2018). Together, these results point toward a synchronization of neural oscillations to the temporal rhythm of the auditory stimulation, which in turn directs peaks of dynamically fluctuating attention to relevant time windows (Henry & Herrmann, 2014). Such an increase in ITPC co-occurred with an increase in magnitude of the sustained activity, which emerges rapidly after the onset of a regularity in auditory stimulation (Herrmann & Johnsrude, 2018) and is associated with enhanced sensitivity to stimulus features (Barascud et al., 2016; Southwell et al., 2017; Southwell & Chait, 2018).

Finally, Andrillon et al. (2015) observed a notable difference between different types of periodic noise, further supporting the claim that perceptual segmentation of noise sequences indeed relies on temporally local features that are idiosyncratic in nature (Andrillon et al., 2015). Specifically, this study contrasted interleaved periodic noise, which consisted of three identical noise segments that were repeated with portions of random noise between them, with seamless periodic noise, in which repeating segments were seamlessly concatenated (labeled “compact” and “diffuse” condition by the authors). These two types of periodicity differ with regard to the length of the repeating noise segment, that is, the time window that listeners could subjectively perceive as repetition onset. This time window is considerably larger in the seamless compared with the

interleaved sequences. Moreover, only in the interleaved condition an unfamiliar random noise portion preceded the onset of the repeating segment in every cycle, whereas the seamless presentation allowed that essentially any time point within the segment could be perceived as the beginning of the repetition. Perceptual learning was evident in both conditions as reflected in an increase in behavioral performance and a stronger inter-trial phase coherence of low-frequency oscillations (0.5–5 Hz). However, a centrally distributed negativity to the onset of the repeating noise segment (i.e., cycle onset) was only observable in the interleaved, but not in the seamless condition. The authors suggested that the event-related responses relative to cycle onset are leveled out on average in the seamless condition due to phase-shifts between subjects who rely on different idiosyncratic features that are temporally distributed over the whole cycle (Andrillon et al., 2015).

1.3 | The present study

The present study sought to disentangle the consistency of perceptual segmentation in periodic noise at the within- and the between-subject level, which were confounded in the analysis of group-level averages as done in previous studies. So far, it remains elusive whether one individual would always perceptually segment a specific, yet unfamiliar stimulus in the same way across multiple presentations, and whether different individuals would perceptually segment the same stimulus in the same way. This separation might advance the understanding of neural processes and mechanisms underlying perceptual segmentation and implicit learning of auditory material that does not contain outstanding acoustic landmarks that could serve as a marker for segmentation.

If listeners indeed rely on subtle idiosyncratic features to perceptually segment periodic noise sequences, as suggested by previous research (Agus et al., 2010; Andrillon et al., 2015), this should be reflected in the following pattern of results: As one person would always perceive the same time point within the repeated noise pattern (at which the chosen feature occurs) as cycle onset, this should result in a high temporal consistency across presentations of the same periodic noise sequence within one individual. Conversely, the subjective repetition onset might be shifted in time between listeners because each of them uses a different subtle feature as a cue for segmentation of the sequence, leading to a low temporal consistency between subjects. To test these assumptions, we conducted an EEG and a behavioral tapping experiment with the same participants. In both our experiments, subjects were presented with the same seamless and interleaved periodic noise sequences as

well as random control sequences. During the EEG experiment, participants performed a periodicity detection task. In the subsequent behavioral tapping experiment, they were asked to tap in synchrony with the perceived rhythm in the auditory stimulus. In addition to the event-related potential (ERP) analysis, aiming at replicating earlier findings (Andrillon et al., 2015), we took a step further by separately analyzing within-subject ITPC of the oscillatory activity (at the frequency of the periodicity in the stimulation) across presentations of the same stimulus and inter-*subject* phase coherence (ISPC). Electrophysiological data were complemented with behavioral markers of coherence in tapping.

2 | METHOD

The study consisted of an EEG experiment and a subsequent behavioral tapping experiment, which were completed by the same participants within one session. All experimental procedures were in accordance with the Declaration of Helsinki.

2.1 | Participants

A total of 24 healthy participants (20 of them female, four male) took part in the study. They were between 18 and 42 years old¹ ($M = 23.71$ years, $SD = 6.17$ years) and three of them were left-handed, the remaining 21 right-handed (as assessed with the short form of the Edinburgh Handedness Inventory; Oldfield, 1971). All of them reported normal hearing, normal or corrected-to-normal vision and no history of any neurological or psychiatric disorder. They received either course credits or monetary compensation (8 € per hour) for their participation. All participants (except one) were naïve regarding the purpose of the study and gave written informed consent before the testing started.

2.2 | EEG experiment

2.2.1 | Stimuli

Gaussian white noise sequences were created using Matlab (version R2019b; The MathWorks Inc.) to serve as auditory stimuli (example stimuli can be found here: https://osf.io/fh4w2/?view_only=a64957ced2d44bfabb6f00a543bd655d).

The sequences were manipulated in terms of their periodicity; that is, they were either seamless, interleaved, or random. Sequence structure is schematically illustrated in Figure 2. Seamless (periodic) sequences consisted of seamlessly concatenated repetitions of a 500 ms noise segment, which is referred to as one cycle. In interleaved (periodic) sequences, a 200 ms noise segment, that is, the first 200 ms of the 500 ms segment used in the corresponding seamless sequence, was repeated every 500 ms and the remaining 300 ms of each cycle were filled with random noise (created anew for each cycle). Random sequences did not contain any temporal regularity or repetition of a noise segment. Seamless and interleaved sequences comprised 10 full cycles and random sequences were matched in duration. Four different, randomly generated 500 ms noise tokens (henceforth called noise patterns) were used to create seamless and corresponding interleaved sequences, respectively. Accordingly, four random noise sequences with a duration of 5000 ms were generated. To temporally separate sequence onset and periodicity onset, a (newly generated) random noise portion, varying in length between 50 and 450 ms, was appended to the beginning of the sequence in each trial, resulting in total sequence durations between 5050 and 5450 ms. Note that periodicity onset refers to the onset of the first presentation of a noise pattern, but the periodicity is only detectable from the onset of the first pattern repetition (i.e., second pattern presentation), called effective periodicity onset in the following.

2.2.2 | Procedure

During the experiment, participants were seated at a table inside an acoustically and electrically shielded cabin. Auditory stimuli were delivered binaurally via headphones (Sennheiser HD-25-1, Sennheiser GmbH & Co. KG) at a sound pressure level (SPL) of approximately 65 decibels (dB) SPL. Stimulus presentation was controlled using the Psychophysics Toolbox extension (PTB-3; Brainard, 1997; Kleiner et al., 2007) in Matlab (version R2016a; The MathWorks Inc.) and participants' behavioral responses were captured with a response time box (Suzhou Litong Electronic Co.).

Before the actual experiment started and after receiving written instructions, subjects had the chance to familiarize themselves with the different types of noise sequences. These were introduced to them as having either a strong rhythm (seamless), a weak rhythm (interleaved), or no rhythm at all (random), with each of those sequence types occurring at equal probability. An example sequence was provided for each type of periodicity and participants could listen to the respective example as often as they

¹Although in the preregistration 40 years was defined as the maximum age for participants, we decided to include data of one subject who was 42 years old to reach our target sample size and finish data collection before the EEG laboratories were closed due to the COVID-19 pandemic.

wanted. During the subsequent experimental blocks, their task was to decide whether a sequence contained any rhythm or not, irrespective of the strength of the rhythm they perceived. They gave responses by pressing either the left or right button on a response time box with their left or right index finger, respectively. Response sides were assigned beforehand and remained the same throughout the whole experiment for one participant, but were counter-balanced across participants. Feedback, that is, percentage of correct responses, was provided at the end of each block.

Each trial started with a fixation cross, which remained on the screen during the presentation of the auditory sequence, concurrently with the sound onset. After the end of the sequence, the response options of the periodicity detection task (“rhythm” and “no rhythm”; in German “Rhythmus” and “Kein Rhythmus”) were shown on the screen until the subject pressed a button or the fixed response interval of 1500 ms expired. To avoid the emergence of a temporal regularity across consecutive sequences, the duration of the silent inter-trial interval, that is, the time between the end of the response period (1500 ms after sequence offset) and the onset of the next sequence, was jittered between 1150 and 1850 ms (in steps of 100 ms).

Trials were arranged in 15 blocks that consisted of 24 trials each. The whole EEG experiment had a duration of about 50 min, excluding breaks, which could be taken between blocks as required. Within each block, each of the four noise patterns (or four specific random sequences) was presented twice in each of the three periodicity conditions, respectively. Trial order was individually randomized, following the restriction that the same periodicity condition must not occur in more than two trials in a row.

2.2.3 | EEG data acquisition

EEG was recorded continuously from 32 active Ag/AgCl electrodes mounted in an elastic cap according to the extended 10–20 system with the following electrode positions: FP1, FP2, AF3, AF4, Fz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, Cz, C3, C4, T7, T8, CP1, CP2, CP5, CP6, Pz, P3, P4, P7, P8, PO3, PO4, Oz, O1, and O2. Additionally, signals were recorded from left and right mastoids (M1, M2), and four electrodes were placed on the outer canthus of each eye and above and below the right eye to capture horizontal and vertical eye movements. One electrode placed on the tip of the nose served for later offline referencing. During preparation, we made sure that all electrode offsets were kept below 30 μ V. An online low-pass filter was applied during recording,

eliminating frequencies above 102.4 Hz. Signals (referenced to the CMS-DRL ground) were amplified with a BioSemi ActiveTwo amplifier (BioSemi B.V.) and digitized with a sampling rate of 512 Hz.

2.2.4 | Data analysis and statistical inference

Behavioral data

Behavioral data were processed in Matlab (version R2019b; The MathWorks Inc.), and statistical analyses were conducted in RStudio (version 3.6.1; RStudio Inc.). Performance in the periodicity detection task was evaluated within the framework of signal detection theory, which is commonly applied to quantify response accuracy in perceptual categorization tasks (MacMillan, 2001). Trials in which the sequence contained a periodicity and participants correctly indicated that they heard a rhythm were defined as hits, while trials in which the sequence did not contain a periodicity, but participants erroneously indicated that they heard a rhythm were counted as false alarms. Hit and false alarm rates were used to compute the sensitivity index d' (applying the so-called log-linear transformation; Hautus & Lee, 2006) separately for each of the four specific noise patterns in seamless and interleaved condition, respectively. To statistically compare periodicity detection performance between seamless and interleaved sequences while taking into account potential effects of different specific noise patterns, a two-way repeated-measures ANOVA with the two-level factor Condition (seamless, interleaved) and the four-level factor Pattern (pattern 1–4) was computed on the d' values using the package “ez” (Lawrence, 2016) in RStudio. Greenhouse–Geisser correction was applied to correct for non-sphericity (as indicated by a significant Mauchly's test with $p < .05$). A significant interaction between the two factors was resolved by splitting up the factorial model by Condition and computing separate one-way ANOVAs with the factor Pattern in both periodicity conditions.

EEG data

EEG data were processed offline in Matlab (version R2019b), using the EEGLAB toolbox (version 2019.0; Delorme & Makeig, 2004) for pre-processing and ERP analysis and the FieldTrip toolbox (Oostenveld et al., 2011) for subsequent cluster-based permutation tests of ERPs. All further statistical analyses were again conducted in RStudio. In a first step, ERPs were analyzed at the group level, including averaging both within and between subjects, with the primary aim to replicate earlier findings with regard to periodicity-related ERPs (Andrillon et al., 2015; Hodapp & Grimm, 2021; Kaernbach et al., 1998). However, we subsequently took a step further to extend previous

findings by calculating phase coherence to additionally analyze consistency of brain responses separately at the within- and between-subject level.

Pre-processing. At first, data were referenced to the reference channel located on the tip of the nose and noisy channels were excluded if their signal variance exceeded an absolute z-score of 3.0. Data of the remaining channels were high-pass and low-pass filtered with Kaiser-windowed sinc finite impulse response (FIR) filters at 0.2 Hz (transition bandwidth: 0.4 Hz, maximum passband deviation: 0.001, filter order: 4638) and 35 Hz (transition bandwidth: 5 Hz, maximum passband deviation: 0.001, filter order: 372). The filtered continuous data were then cut into epochs that ranged from 100 ms before to 6000 ms after sequence onset, that is, approximately 500 ms after sequence offset. Following this, an independent component analysis (ICA) was used to clean the data from physiological and technical artifacts. To improve the signal-to-noise ratio for decomposition, ICA was computed on a copy of the data that had been filtered with a 1 Hz high-pass filter (transition bandwidth: 0.5 Hz, maximum passband deviation: 0.001, filter order: 3710) and the same 35 Hz low-pass filter and epoched as described above. Epochs whose maximal peak-to-peak difference exceeded 750 μ V were excluded from the ICA decomposition and the data were down-sampled to 128 Hz to shorten computation time. Subsequently, ICA weights, obtained with an infomax algorithm implemented in EEGLAB's *runica* function, were transferred to the EEG data set pre-processed with the final parameters and independent components were classified using the IC Label plugin for EEGLAB (Pion-Tonachini et al., 2019). Artefactual components classified as eye blinks, muscle activity, cardiac activity, line noise or channel noise were removed. Finally, previously identified and excluded noisy channels were spherically spline interpolated (using the *sphspline* plugin for EEGLAB, authored by Andreas Widmann; <https://github.com/widmann/sphspline>).

Event-related potential analysis. For the analysis of periodicity-related ERPs within single cycles, shorter epochs were extracted that ranged from -100 to 500 ms relative to cycle onset (or corresponding time points in random noise sequences). The first and the last cycle of each sequence were excluded to minimize the influence of sequence onset and offset effects, which resulted in eight remaining cycles per sequence. Epochs were baseline-corrected to the 100 ms interval before cycle onset and all epochs in which amplitudes exceeded a 150 μ V peak-to-peak difference were discarded from further analysis. The remaining epochs were re-referenced to the algebraic

mean of the two mastoid electrodes (M1, M2) and averaged separately for each periodicity condition, first split by the specific noise patterns (with an average of 236 ± 8 [$M \pm SD$] epochs included per noise pattern and periodicity condition within each subject) and then pooled across them. Finally, grand averages across participants were computed from the within-subject averages (using the *grandaverage* plugin for EEGLAB, authored by Andreas Widmann; <https://github.com/widmann/grandaverage>), again once separately for each noise pattern and once pooled across noise patterns within one periodicity condition.

Differences in amplitude between periodicity conditions were analyzed statistically at the level of averages across the four noise patterns. Non-parametric cluster-based permutation tests were used to identify clusters of significant amplitude differences between conditions that pointed into the same direction in temporally and spatially adjacent samples (Maris, 2012; Maris & Oostenveld, 2007). In total, three cluster-based permutation tests (with an alpha level and cluster alpha of 0.05, respectively, using a Monte Carlo approximation involving 1000 permutations to estimate cluster-level significance probability) were performed for pairwise comparisons between the three periodicity conditions in a time window that covered the entire cycle (0–500 ms relative to cycle onset). Three non-overlapping time windows of equal length (100 ms) were defined after visually inspecting the results of the pairwise cluster-based permutation tests, the first one ranging from 0 to 100 ms, the second one from 100 to 200 ms and the third one from 250 to 350 ms relative to cycle onset. For each of these time windows, mean amplitudes were extracted at electrode Fz for each periodicity condition, in line with the frontocentral distribution of the current ERP topographies as well as with earlier reports of periodicity-related ERPs in noise (Andrillon et al., 2015; Berti et al., 2000; Kaernbach et al., 1998). Mean amplitudes were compared between the conditions by means of a two-way repeated measures ANOVA with the three-level factors Condition (seamless, interleaved, random) and Time Window (0–100, 100–200, 250–350 ms). Where applicable, correction for non-sphericity was used as described above. A significant interaction between the two factors was resolved by splitting up the factorial model by Time Window and computing separate one-way ANOVAs with the factor Condition for each time window, followed by pairwise paired sample *t*-tests between the periodicity conditions whenever the main effect of Condition reached significance in a follow-up ANOVA. To account for multiple comparisons, *p*-values of these post-hoc *t*-tests were adjusted based on the false discovery rate (FDR; Benjamini & Hochberg, 1995).

Phase coherence analysis. When looking at grand average ERPs at the group level only, temporal consistency of brain responses within and between participants are confounded and cannot be disentangled. Therefore, we additionally analyzed phase coherence of oscillatory EEG activity evoked by the periodicity in the presented noise sequences separately at the within- and at the between-subject level. To this end, ITPC across trials within each participant and ISPC across participants within trials were computed in two parallel analyses as described below.

For analyses in the frequency domain, epochs were extracted that ranged from effective periodicity onset to periodicity offset, that is, 500–5000 ms relative to the onset of the first noise pattern presentation. Exactly 26 artifact-free epochs were included for each subject, for each periodicity condition, and for each noise pattern, which were then demeaned and multiplied with a Hanning window to reduce $1/f$ noise. Fast Fourier transforms (FFTs) were computed at the single-trial level to extract phase information. In two parallel analyses, ITPC within each subject and ISPC between subjects were estimated from the resulting phase angles.ⁱⁱ

ITPC at the frequency f was computed for each subject (separately for each channel, each periodicity condition and each noise pattern) using the following formula:

$$\text{ITPC}(f) = \frac{1}{N_{\text{tr}}} \sum_{k=1}^{N_{\text{tr}}} e^{i\phi^k(f,t)}, \quad (1)$$

where N_{tr} is the number of trials (i.e., 26) and ϕ^k is the phase angle of the oscillatory signal (in radians) in the current trial.

Analogously, ISPC at the frequency f was computed for each trial (separately for each channel, each periodicity condition and each noise pattern) using the following formula:

$$\text{ISPC}(f) = \frac{1}{N_{\text{subj}}} \sum_{k=1}^{N_{\text{subj}}} e^{i\phi^k(f,t)}, \quad (2)$$

where N_{subj} is the number of subjects (i.e., 24) and ϕ^k is the phase angle of the oscillatory signal (in radians) in the current subject.

ⁱⁱ This procedure deviates from our preregistration. We decided to deviate from our original analysis plan in order to streamline our analyses in the main manuscript. Nevertheless, we also carried out all analyses as preregistered and report the results in detail here: https://osf.io/gcfrt/?view_only=424a4da5f612461f980e8e1cbad81612. Taken together, both analysis approaches yielded a virtually identical pattern of results and lead to the same conclusions.

Subsequently, ITPC and ISPC maps were averaged across the different noise patterns within each periodicity condition to improve signal-to-noise ratio. ITPC and ISPC coefficients were extracted at the frequency of interest (2 Hz) at electrode Fz. To eliminate potential differences between conditions in the overall level of phase coherence across frequencies, ITPC and ISPC coefficients were referenced to the average of two neighboring reference frequencies (chosen symmetrically at the edges of the peak around 2 Hz, i.e., 1.66 and 2.44 Hz). Independent one-way repeated measures ANOVAs with the three-level factor Condition (seamless, interleaved, random) were computed for ITPC and ISPC coefficients, respectively. A significant main effect of Condition was followed up by pairwise paired-sample t -tests between the three periodicity conditions. Where applicable, correction for non-sphericity was used, and multiple comparisons were accounted for as described above.

2.3 | Tapping experiment

2.3.1 | Stimuli

Seamless and interleaved noise sequences were generated following the same procedure as described above and based on the very same four specific noise tokens. However, sequences consisted of 30 (instead of 10) full cycles with a total duration of 15 s after an initial portion of random noise that varied in length between 50 and 450 ms. Fifteen exemplars (with an individual random noise portion in the beginning) were created for each of the four noise patterns in seamless and interleaved condition, respectively. Additionally, control sequences (of the same duration as seamless and interleaved sequences) that contain temporally regular physical changes in a random noise signal were created by increasing a 1 ms segment of noise in intensity by approximately 12 dB every 500 ms. These short intensity increases are usually perceived as a clicking sound in the noise. This control condition was used to obtain an estimate of how precisely participants can synchronize their tapping with the auditory input if there is an obvious acoustic cue in the stimulus. Twenty-four exemplars of control sequences were created, each of them with an individual random noise portion of varying duration (between 50 and 450 ms) inserted before the first click.

2.3.2 | Procedure

Following the EEG experiment, after a short break of approximately 15 minutes participants were again seated

at a table inside an acoustically and electrically shielded cabin. The experimental settings with regard to auditory stimulus presentation were the same as for Experiment 1. Participants' taps were captured using a custom-made device consisting of a force sensing resistor (FSR406; Interlink Electronics) attached to an acrylic sheet with foam rubber padding and connected to a microcontroller (Teensy 3.2; PJRC). When subjects tapped on the pad and the measured force increase exceeded a reasonable threshold, the microcontroller sent a trigger corresponding to tap onset, which was captured by the Psychophysics Toolbox with a sampling rate of 1000 Hz.

Participants were asked to deliberately pay attention to the rhythm in the presented noise sequences and focus on a characteristic feature in the sound that reoccurs periodically. As soon as they had identified such a recurring feature in the noise, they should tap, as synchronously with the perceived rhythm as possible, with the index finger of their dominant hand on the tapping pad placed on the table in front of them. They were instructed to start tapping after a few seconds in every trial, even if the rhythm was only very subtle, and to continue tapping until the end of the sequence. Before the start of the actual experimental trials, subjects could familiarize themselves with the task during a short block of five exemplary periodic sequences (three seamless, followed by two interleaved sequences).

Each trial, starting with sound onset, had a maximum duration of 15.45 s, corresponding to the maximum length of any auditory sequence. However, most of the trials were shorter as sound presentation stopped and the trial was aborted as soon as the participant had tapped 10 times. To avoid the emergence of a temporal regularity across consecutive sequences, the duration of the silent inter-trial interval was jittered between 1650 and 2350 ms (in steps of 100 ms).

Trials were arranged in six blocks that consisted of 24 trial each. The total duration of the tapping experiment was about half an hour, excluding breaks, which could be taken between blocks as required. All 24 control sequences containing regular physical changes were presented in the last block. Within each of the first five blocks, each of the four noise patterns was presented three times in each of the two periodicity conditions. Trial order was individually randomized, following the restriction that the same periodicity condition must not occur in more than three trials in a row.

2.3.3 | Data analysis and statistical inference

Data processing was again done in Matlab (version R2019b) and statistical analyses were conducted in RStudio.

Tapping data were analyzed in terms of two measures: tapping rate and tapping phase. While inter-tap intervals, that is, the time elapsing between the onsets of two consecutive taps, as a measure of tapping rate only reflects how strictly the (2-Hz) rhythm is kept, tapping phase (relative to cycle onset) additionally provides information about how consistently participants tap at a similar time point within the cycle across trials. For both analyses, all trials in which participants tapped less than 10 times were discarded. On average, less than one trial was excluded per noise pattern in seamless and interleaved condition and in the control condition for each subject.

Tapping rate

Mean and standard deviation of the intervals between two consecutive taps were computed for each participant, separately for each of the four noise patterns in seamless and interleaved condition and for the control (click) condition. To reduce the influence of single outliers within a sequence of temporally regular taps, implausible inter-tap intervals below 100 ms or above 1000 ms were excluded. Standard deviation of the inter-tap intervals was compared statistically between periodicity conditions, reflecting the amount of variability in the tapping rhythm. Concretely, a small standard deviation indicates that the rhythm is kept consistently without much variation in the inter-tap interval duration (within and between trials) and a larger standard deviation points toward rather inconsistent tapping with varying inter-tap interval duration. A repeated measures ANOVA with the three-level factor Condition (seamless, interleaved, click) was computed with the standard deviations of the inter-tap intervals, using averages across all four noise patterns in seamless and interleaved condition, respectively. A significant main effect of Condition was followed up by pairwise paired-sample *t* tests between the three periodicity conditions. To shed light on whether specific noise patterns differentially influence tapping rate in seamless and interleaved sequences, an additional two-way repeated measures ANOVA with the two-level factor Condition (seamless, interleaved) and the four-level factor Pattern (pattern 1–4) was computed. A significant interaction between the two factors was resolved by splitting up the factorial model by Condition and computing separate one-way ANOVAs with the factor Pattern for seamless and interleaved condition. Where applicable, correction for non-sphericity was used as described above.

Tapping phase

As a measure of tapping asynchrony, we calculated the phase for each of the 10 tap times within a sequence

relative to a 2-Hz signal (aligned to the rhythm of stimulus cycle onsets), constrained to the range -250 to 250 ms (corresponding to $-\pi$ to π). Mean preferred phase angles were computed across the 10 taps within a trial. Tapping phase coherence (*tapPC*) across trials was estimated for each participant, separately for each of the four noise patterns in seamless and interleaved condition and for the control (click) condition, using the following formula:

$$\text{tapPC} = \frac{1}{N_{\text{tr}}} \sum_{k=1}^{N_{\text{tr}}} e^{i\phi^k}, \quad (3)$$

where N_{tr} is the number of trials and ϕ^k is the mean phase angle of the taps (in radians) in the current trial.

Tapping phase coherence was statistically compared between the three periodicity conditions and between different specific noise patterns in seamless and interleaved conditions by means of analogous statistical procedures as used for the analysis of inter-tap intervals.

In previous literature, tapping asynchrony was often measured as the time difference between response and stimulus (Aschersleben, 2002; Repp, 2005; Repp & Su, 2013). As the assignment of individual taps to a specific feature in the stimulation is not trivial in the absence of an objective time point that constitutes the beat in our periodic noise sequences, we instead used tapping phase to approximate tapping asynchrony (as described above). Nevertheless, in line with our preregistration, we also analyzed tapping asynchrony following the established approach and report the results here: https://osf.io/gcfrt/?view_only=424a4da5f612461f980e8e1cbad81612. As expected, both approaches yield a very similar pattern of results.

2.4 | Brain-behavior correlations

After analyzing EEG data and tapping data separately, they were combined into one analysis. Brain-behavior correlations were computed to evaluate the relationship between brain responses and behavioral responses to periodicity in noise sequences and, in particular, their consistency. Specifically, it should be tested whether participants whose brain activity is more coherently phase-locked to the periodicity in the stimulation also tend to tap more synchronously across trials by correlating phase coherence of brain responses with phase coherence of tapping to the same periodic noise sequence. Pearson correlations were computed (in RStudio) between individual ITPC coefficients and tapping phase coherence coefficients, both averaged across the four specific noise patterns (after Shapiro–Wilk normality tests had shown that all values were normally distributed; all W 's > 0.93 and uncorrected

p 's $> .155$). The two correlation coefficients were then statistically tested against zero and p -values were adjusted for multiple comparisons (based on the FDR as above). Finally, the coefficients were z -transformed to compare them statistically with each other.

3 | RESULTS

3.1 | EEG experiment

3.1.1 | Behavioral data: periodicity detection performance

In general, participants were able to successfully detect periodicity in noise sequences and (on average) performed above chance for all four noise patterns in both periodic conditions. However, sensitivity in the periodicity detection differed systematically between conditions and noise patterns (see Figure 1). Participants were overall more sensitive in detecting periodicity in seamless than in interleaved sequences (main effect of Condition: $F[1, 23] = 70.57$, $p < .001$, partial $\eta^2 = 0.75$). When resolving the Condition \times Pattern interaction ($F[3, 69] = 13.25$, $p < .001$, partial $\eta^2 = 0.37$), performance was found to differ significantly between noise patterns only in the interleaved condition (main effect of Pattern: $F[3, 69] = 16.63$, $p < .001$, partial $\eta^2 = 0.42$) with pattern 3 standing out from the others and reaching the performance level of the seamless condition. Conversely, performance was equally near-perfect for all noise patterns in the seamless condition (main effect of Pattern: $F[3, 69] = 1.42$, $p = .253$, partial $\eta^2 = 0.06$).

3.1.2 | Event-related responses to periodicity in noise

As shown in Figure 2, event-related responses to the noise sequences were clearly modulated by the periodicity of the sequences. A negative potential emerged after periodicity onset, remained relatively sustained between 500 and 2000 ms before gradually decreasing toward the end of the sequence (which along with an offset response). The onset of the sustained period corresponds to the effective periodicity onset, that is, the onset of the first noise pattern repetition. Note that the typical sound onset response is leveled out because sound onset is jittered due to the varying length of the initial random portion before periodicity onset. During the sustained period, the negativity was notably stronger in both seamless and interleaved compared with the random condition, and particularly strong in response to seamless sequences. Importantly, on top of

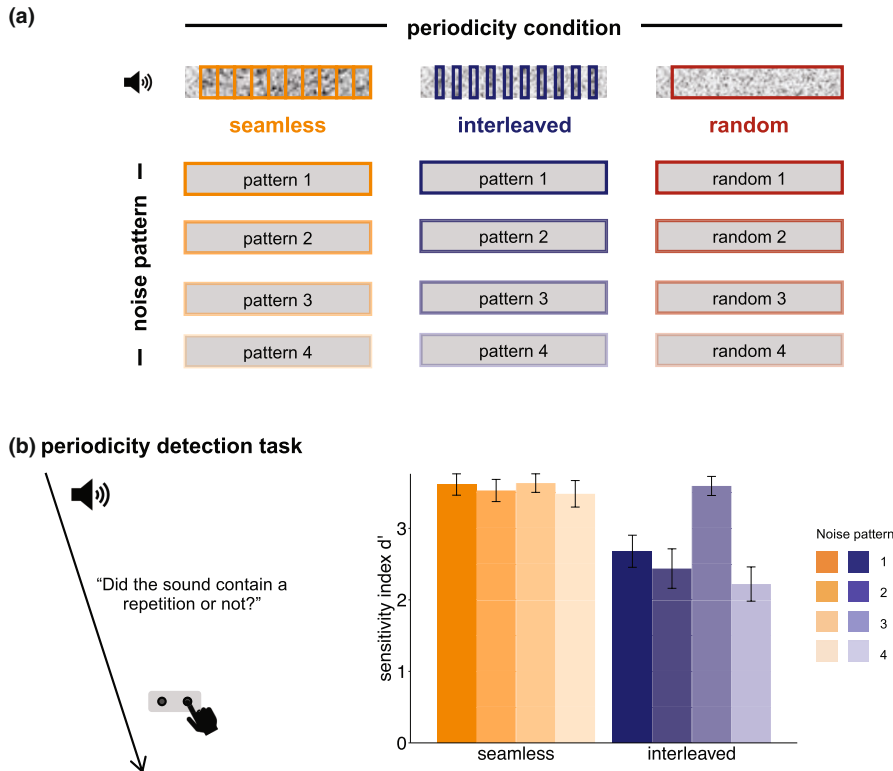


FIGURE 1 (a) Illustration of the stimulus design. Seamless and interleaved periodic sequences were created from four specific noise patterns, and four random sequences were created with the same length. (b) Left panel: Schematic illustration of the periodicity detection task. Right panel: Behavioral periodicity detection performance as measured by the mean sensitivity index d' for each noise pattern in seamless and interleaved condition, respectively. Error bars indicate ± 1 standard error of means (SEM).

the sustained response, a 2-Hz oscillatory modulation was observed in the interleaved condition, corresponding to the periodicity frequency of the stimulation.

Zooming into single cycles, periodicity-related ERPs were elicited time-locked to the onset of a periodically recurring noise pattern, which resulted in the cyclic ERP activity over the course of the sequence (see Figure 3). On average across noise patterns, a frontocentral negativity emerged between 100 and 300 ms relative to cycle onset in the seamless condition, peaking at approximately 200 ms. In the interleaved condition, a broadly distributed and frontocentrally pronounced negativity occurred somewhat later between 150 and 400 ms, with a peak at approximately 300 ms after cycle onset, but was clearly stronger than in the seamless condition. Additionally, this prominent negativity was preceded by an earlier positivity within the first 100 ms after cycle onset. In contrast to both periodic conditions, no systematic negative or positive deflections were evoked relative to corresponding time points in random sequences. Statistical evaluation of mean ERP amplitudes revealed that the differences in ERP amplitude between periodicity conditions changed systematically over the course of the cycle (Condition \times Time Window interaction: $F[4, 92] = 54.88$, $p < .001$, partial $\eta^2 = 0.70$). ERP amplitude effects will be described for each of the three time windows in turn:

In the first time window, covering the first 100 ms after cycle onset, an early positivity was evoked in response

to cycle onset only for interleaved, but not for seamless and random sequences (main effect of Condition: $F[2, 46] = 10.02$, $p < .001$, partial $\eta^2 = 0.30$). Concretely, amplitudes differed significantly between interleaved and random ($t[23] = 3.81$, adjusted $p = .002$, $d = 0.78$) as well as between interleaved and seamless ($t[23] = 3.75$, adjusted $p = .002$, $d = 0.77$), but not between seamless and random condition ($t[23] = -1.50$, adjusted $p = .146$, $d = 0.31$).

In the second time window, ranging from 100 to 200 ms relative to cycle onset, a negativity emerged in both seamless and interleaved compared with the random condition ($F[2, 46] = 12.37$, $p < .001$, partial $\eta^2 = 0.35$). Although amplitudes did not differ significantly between the two periodic conditions ($t[23] = 1.59$, adjusted $p = .127$, $d = 0.32$), they did so between seamless and random ($t[23] = -5.28$, adjusted $p < .001$, $d = 1.08$) and between interleaved and random condition ($t[23] = -3.50$, adjusted $p = .003$, $d = 0.71$).

Finally, in the third time window, ranging from 250 to 350 ms after cycle onset, the negative deflection, evoked in both periodic conditions compared with the random condition, was remarkably stronger in the interleaved than in the seamless condition. Concretely, amplitudes were found to differ significantly between seamless and random ($t[23] = -2.59$, adjusted $p = .016$, $d = 0.53$), interleaved and random ($t[23] = -9.40$, adjusted $p < .001$, $d = 1.92$) and interleaved and seamless condition ($t[23] = -8.13$, adjusted $p < .001$, $d = 1.66$).

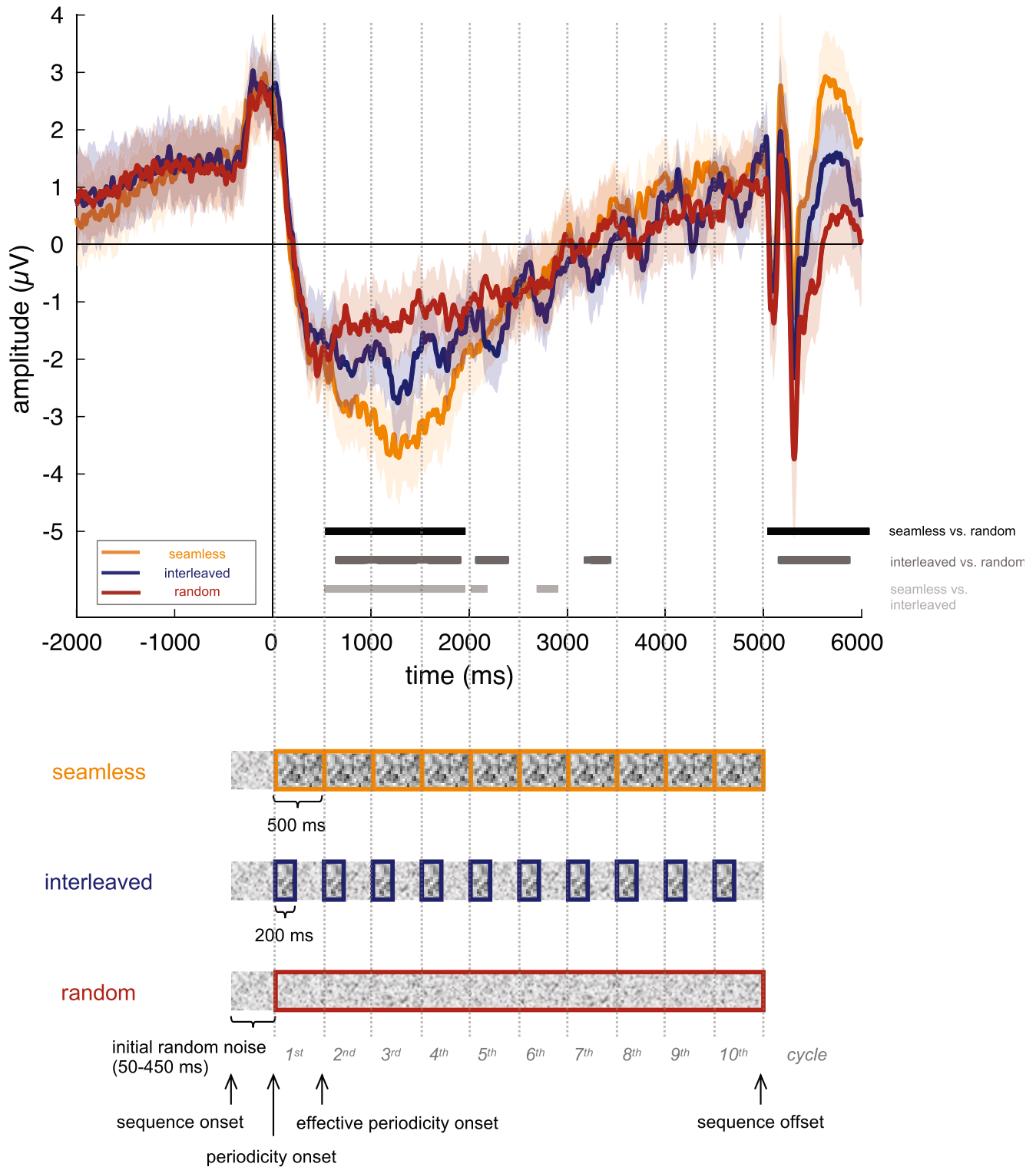


FIGURE 2 Event-related responses relative to periodicity onset (at 0 ms) at electrode Fz for the three periodicity conditions. Note that periodicity onset refers to the first presentation of a noise pattern that is repeated periodically throughout the sequence and the sound onset is jittered between -450 ms and -50 ms. For visualization purposes, data were high-pass filtered with a lower cut-off of 0.05 Hz (transition bandwidth: 0.1 Hz, maximum passband deviation: 0.001, filter order: 18546) and referenced to the average of all channels. Trials in which the peak-to-peak amplitude difference exceeded $300 \mu\text{V}$ were discarded and no baseline was used. Shaded areas indicate ± 1 SEM. Horizontal bars under the ERP curves indicate a significant difference in amplitude between the respective conditions as revealed by pairwise cluster-based permutation tests (using the same parameters as described above for the level of single cycles). The structure of the noise sequences for each periodicity condition is illustrated schematically below the ERP plot.

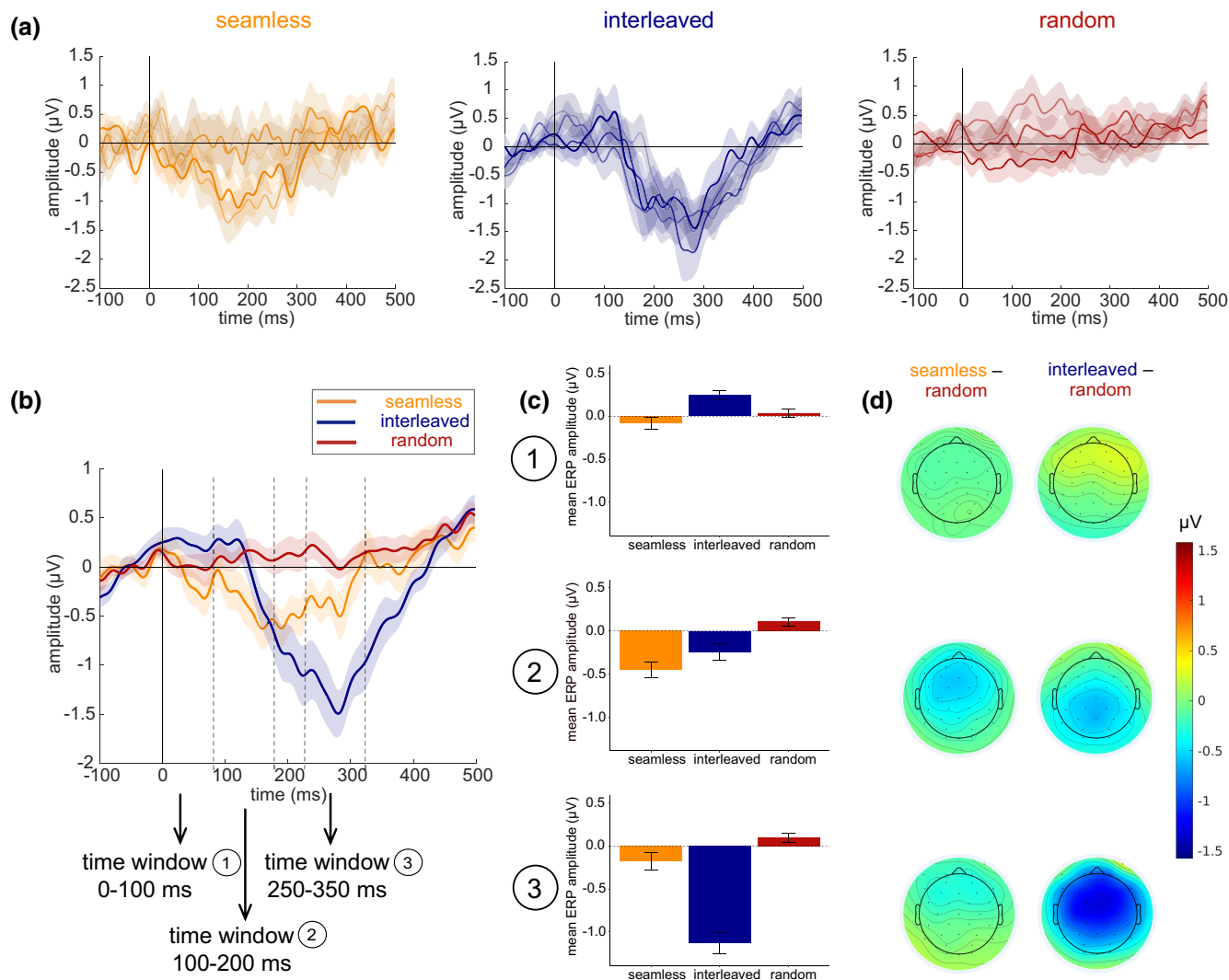


FIGURE 3 Results of the event-related potential analysis. (a) Noise pattern-wise event-related responses relative to cycle onset (at 0 ms) for the three periodicity conditions. (b) Averaged event-related responses across noise patterns relative to cycle onset (at 0 ms). (c) Mean amplitudes for the three periodicity conditions in the three relevant time windows. (d) Topographies of difference potentials (periodic minus random) in each of the three time windows for seamless and interleaved condition, respectively. Shaded areas in the ERP plots and error bars in the bar plots indicate ± 1 SEM.

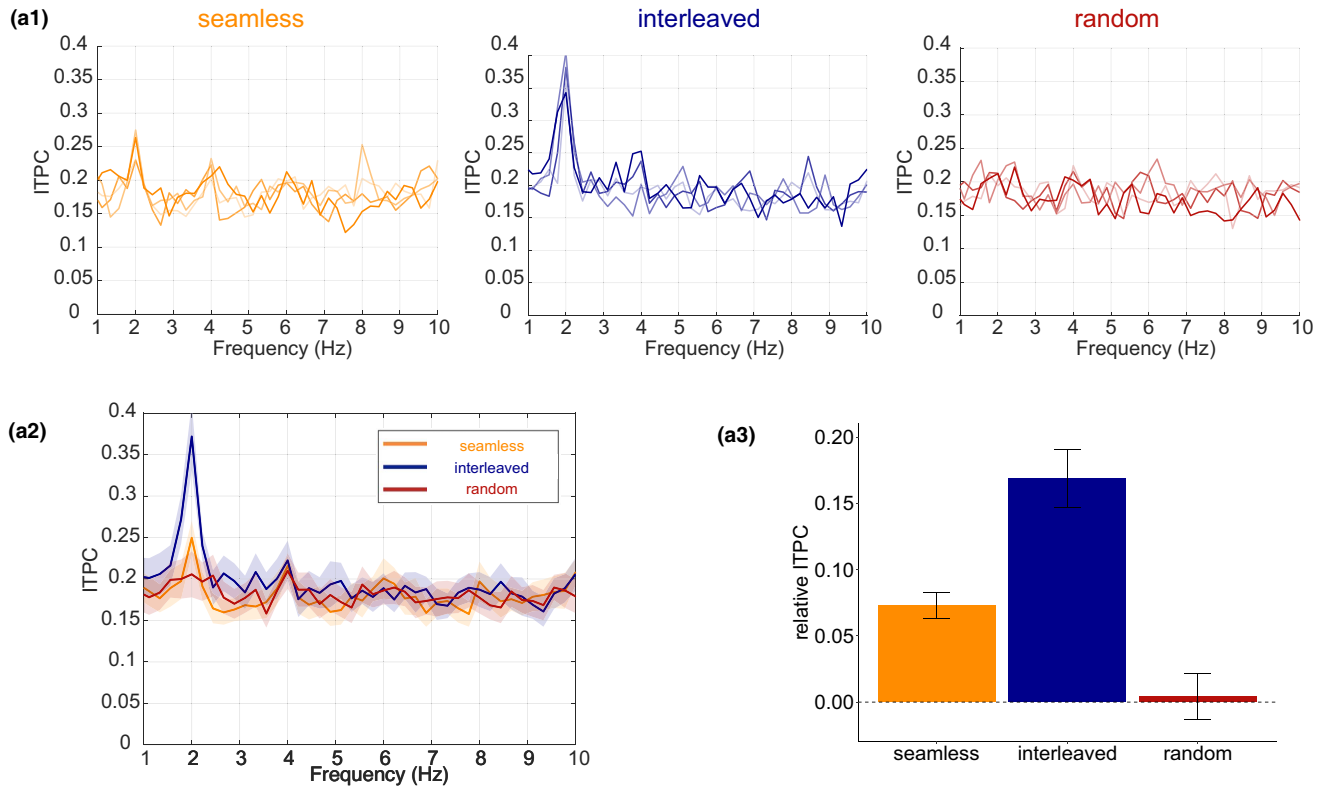
Interestingly, while a prominent negativity, preceded by an early positivity, was elicited very consistently for all four noise patterns in the interleaved condition, there were notable differences between noise patterns in the seamless condition. A negativity was apparent only for two out of four patterns (pattern 1 and pattern 3), whereas there was no obvious (positive or negative) deflection at any time point within the cycle for the other two patterns.

3.1.3 | Oscillatory brain activity at the periodicity frequency

At the within-subject level, ITPC showed a clear peak around 2 Hz, corresponding to the frequency of the

periodicity in the stimulation, in the interleaved condition and a somewhat smaller peak in the seamless condition, whereas no such peak was observable in the random condition (see Figure 4, Panel a). The statistical evaluation revealed that ITPC differed significantly between conditions ($F[2, 46] = 22.48, p < .001, \text{partial } \eta^2 = 0.50$). Specifically, ITPC was significantly stronger in the interleaved compared with both seamless ($t[23] = 4.21, \text{adjusted } p = .001, d = 0.86$) and random condition ($t[23] = 5.62, \text{adjusted } p < .001, d = 1.15$). Moreover, it was significantly stronger in the seamless than in the random condition ($t[23] = 3.36, \text{adjusted } p = .003, d = 0.69$). A peak in phase coherence at 2 Hz was observable for each specific noise pattern in both periodic conditions. Taken together, at the within-subject level, both seamless and interleaved noise sequences

inter-TRIAL phase coherence



inter-SUBJECT phase coherence

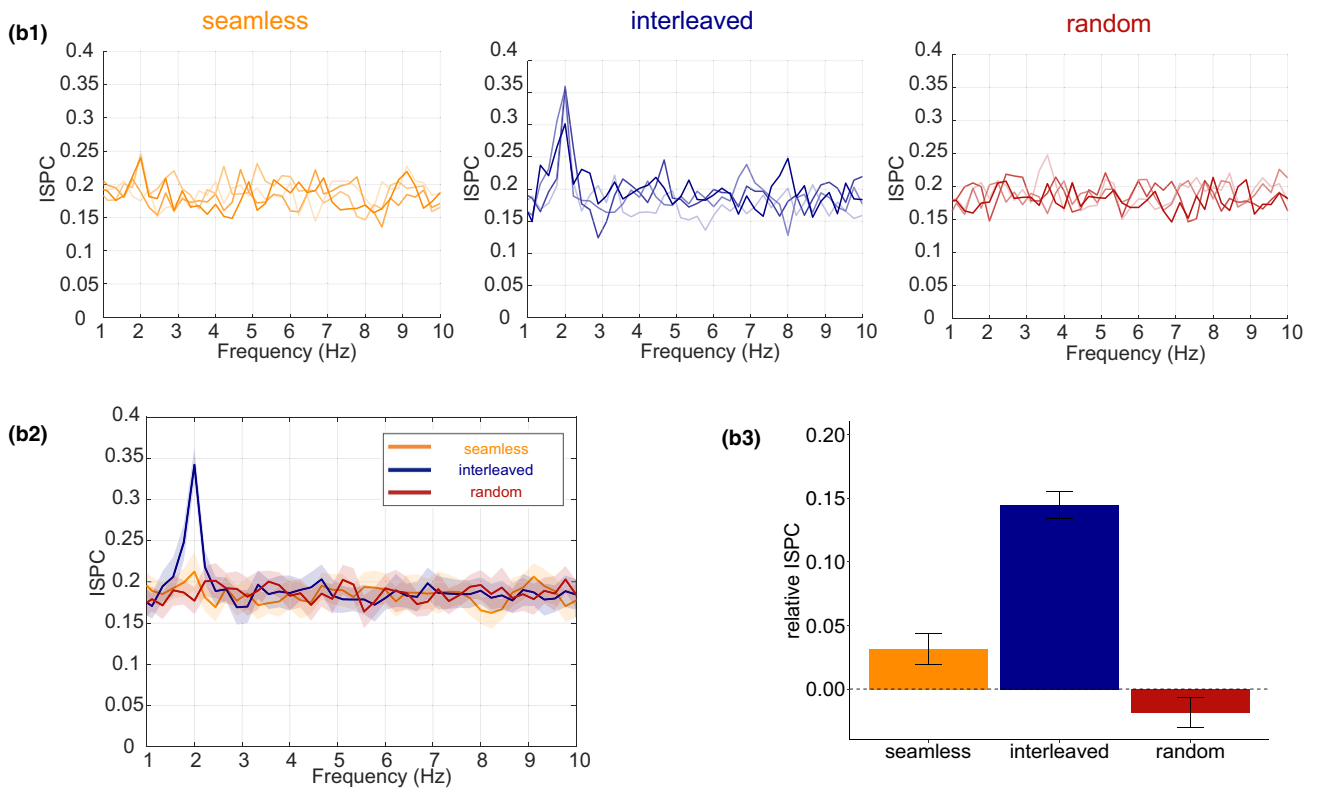


FIGURE 4 Legend on next page

FIGURE 4 Results of the phase coherence analysis. (a) Extracted coefficients over frequencies at electrode Fz for each noise pattern separately (a1), averaged coefficients across noise patterns (a2) and mean coefficients at 2 Hz (a3) of within-subject inter-trial phase coherence. (b) Extracted coefficients over frequencies at electrode Fz for each noise pattern separately (b1), averaged coefficients across noise patterns (b2) and mean coefficients at 2 Hz (b3) of between-subject inter-subject phase coherence. Shaded areas in the ITPC and ISPC plots and error bars in the bar plots indicate ± 1 SEM.

induced substantial phase coherence of oscillatory activity at the periodicity frequency that was particularly strong for interleaved sequences.

At the between-subject level, ISPC showed a clear peak around 2 Hz in the interleaved condition, whereas there was only a smaller peak in the seamless condition and no peak in the random condition (see [Figure 4](#), Panel b). The statistical evaluation revealed that ISPC differed significantly between conditions ($F[2, 50] = 43.76$, $p < .001$, partial $\eta^2 = 0.64$). Specifically, ISPC was significantly stronger in the interleaved compared both seamless ($t[25] = 5.84$, adjusted $p < .001$, $d = 1.15$) and random condition ($t[25] = 9.35$, adjusted $p < .001$, $d = 1.83$). Moreover, it was significantly stronger in the seamless than in the random condition ($t[25] = 2.99$, adjusted $p = .006$, $d = 0.59$). A peak in phase coherence at 2 Hz was observable for each specific noise pattern in the interleaved condition. In the seamless condition, however, a clear peak at 2 Hz was only elicited by two (pattern 1 and pattern 3), but not by the remaining two patterns, resulting in the small 2-Hz peak on average across noise patterns. Taken together, at the between-subject level, interleaved sequences induced substantial phase coherence of oscillatory activity at the periodicity frequency, whereas this was only the case for specific noise patterns in the seamless condition.

3.2 | Tapping experiment

3.2.1 | Tapping rate

At the level of averages across noise patterns, periodicity conditions differed significantly in terms of the standard deviation of inter-tap intervals (main effect of Condition: $F[2, 46] = 11.34$, $p < .001$, partial $\eta^2 = 0.33$; see [Figure 5](#), Panel a). Concretely, the variation in inter-tap interval duration was significantly larger in the interleaved condition compared with both seamless ($t[23] = 4.24$, adjusted $p = .001$, $d = 0.87$) and click condition ($t[23] = 2.99$, adjusted $p = .010$, $d = 0.61$), while it did not differ between seamless and click condition ($t[23] = -1.45$, adjusted $p = .162$, $d = 0.30$). Results of the analysis comparing the specific noise patterns in seamless and interleaved condition again suggested larger variation in inter-tap intervals in the interleaved compared with the seamless condition (main effect of Condition: $F[1, 23] = 17.97$, $p < .001$, partial $\eta^2 = 0.44$) that was independent of specific noise patterns

(main effect of Pattern: $F(3, 69) = 2.64$, $p = .056$, partial $\eta^2 = 0.10$; Condition \times Pattern interaction: $F(3, 69) = 1.47$, $p = .239$, partial $\eta^2 = 0.06$). These findings indicate that participants kept the 2-Hz rhythm less consistently when tapping to interleaved sequences compared with seamless sequences (where they tapped as consistently as they did to sequences containing regular physical cues in the signal).

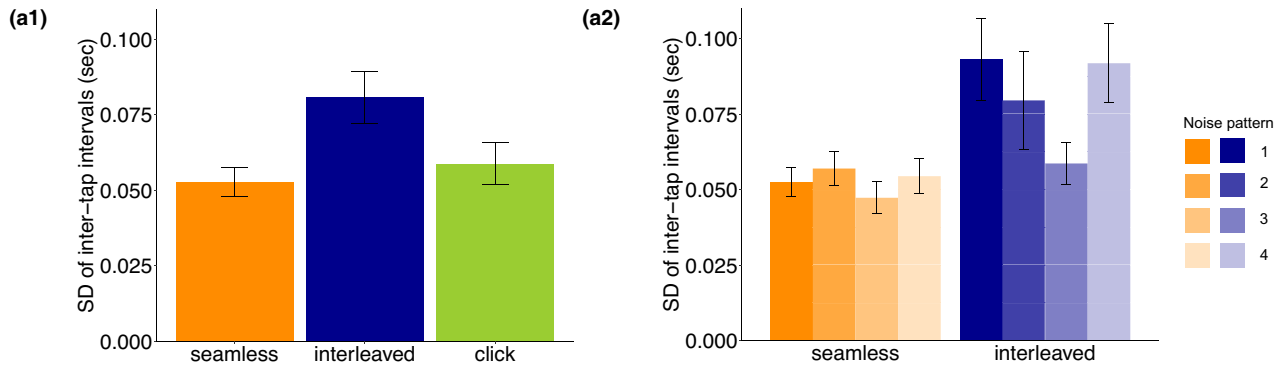
3.2.2 | Tapping phase

At the level of averages across noise patterns, tapping phase coherence differed significantly between periodicity conditions (main effect of Condition: $F[2, 46] = 40.42$, $p < .001$, partial $\eta^2 = 0.64$; see [Figure 5](#), Panel b). Specifically, participants' tapping was more coherent in the click condition than in both seamless ($t[23] = -8.04$, adjusted $p < .001$, $d = 1.64$) and interleaved condition ($t[23] = -8.05$, adjusted $p < .001$, $d = 1.64$). No significant difference was found between seamless and interleaved condition ($t[23] = 1.08$, adjusted $p = 0.290$, $d = 0.22$). The analysis comparing the specific noise patterns in seamless and interleaved condition again found no significant difference between the two periodic conditions (main effect of Condition: $F[1, 23] = 1.16$, $p = .293$, partial $\eta^2 = 0.05$) and, furthermore, suggested that specific noise patterns did not systematically influence tapping phase coherence (main effect of Pattern: $F(3, 69) = 1.34$, $p = .268$, partial $\eta^2 = 0.06$; Condition \times Pattern interaction: $F(3, 69) = 1.52$, $p = .217$, partial $\eta^2 = 0.06$). These findings indicate that subjects tapped less coherently to a subtle periodicity in noise sequences than they did to temporally regular physical changes (clicks) in the auditory stimulus across trials, while their tapping was similarly coherent for both types of periodicity.

3.3 | Correlation of EEG responses and behavior

Phase coherence of brain responses and of tapping showed no particular association in either periodic condition (seamless: $r = -0.082$; interleaved: $r = 0.120$). Pearson correlation coefficients fell short of statistical significance in both seamless ($t[22] = -0.38$, adjusted $p > .999$) and interleaved condition ($t[22] = 0.57$, adjusted $p > .999$), and

inter-tap intervals: standard deviation



tapping phase coherence

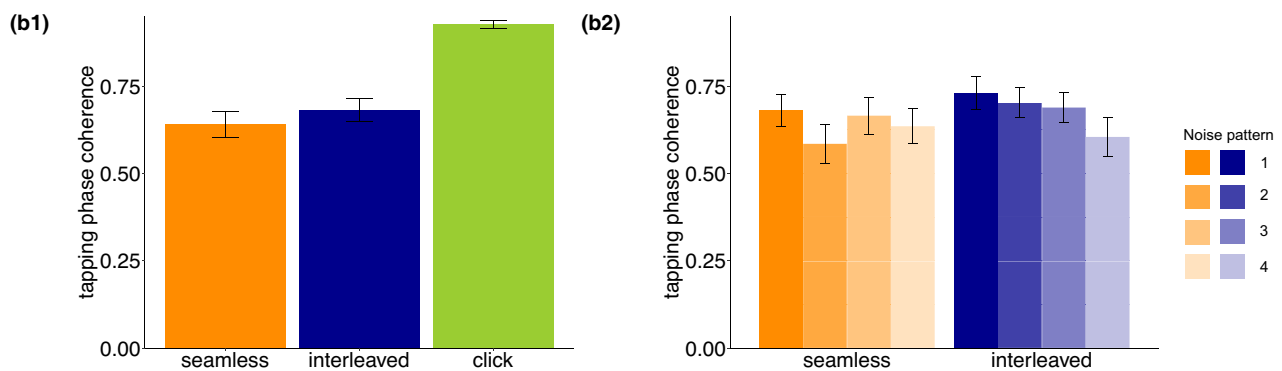


FIGURE 5 Behavioral tapping performance. (a) Standard deviations of the inter-tap intervals as a measure of tapping rate consistency averaged across noise patterns (a1) and for each noise pattern separately (a2). (b) Mean tapping phase coherence averaged across noise patterns (b1) and for each noise pattern separately (b2). Error bars indicate ± 1 SEM.

the two coefficients did not significantly differ from each other ($z = -0.66, p = .512$).

4 | DISCUSSION

The aim of the present combined EEG and behavioral tapping study was to shed light on the consistency of perceptual segmentation of unstructured auditory material within and between listeners. To this end, participants were presented with seamless and interleaved periodic noise sequences. Both types of sequences contained repetitions of a specific noise segment, but differed with regard to the length of the repeating noise segment and with regard to the fine-structure of the sequence (i.e., whether or not a portion of random noise was inserted between the pattern repetitions). Specifically, the time window that listeners could subjectively perceive as repetition onset was shorter and followed a portion of unfamiliar random noise in interleaved in contrast to seamless sequences. The analysis of phase coherence that was carried out separately at the within- and

between-subject level allowed us to disentangle consistency within and across individuals.

4.1 | Periodicity perception in noise

We found that listeners did perceive the periodicity in both seamless and interleaved sequences. This was reflected at the behavioral level in an above-chance periodicity detection performance and a highly consistent tapping rate. At the electrophysiological level, we observed a sustained response relative to (effective) periodicity onset that showed increased amplitudes for periodic (compared with random) noise sequences, and characteristic evoked responses relative to the repeating pattern onsets within the periodic sequences. The pattern of differences between seamless and interleaved sequences suggests that these behavioral and electrophysiological markers reflect two different aspects of periodicity perception: While periodicity detection performance, stability of the tapping rhythm and magnitude of the sustained response all seem to point toward

a stronger percept of periodicity in seamless sequences, more prominent evoked responses relative to pattern onsets and stronger phase coherence within and between listeners indicated more consistent temporal anchoring in the interleaved condition.

Although well above chance in both conditions, perceptual sensitivity in the periodicity detection task was considerably decreased in interleaved compared with seamless sequences. This is in line with previous reports, which, for instance, showed that listeners detect recurring noise patterns more readily the longer they are in duration (for durations increasing from 200 to 500 ms; Rajendran et al., 2016). Furthermore, the tapping rate reflected that periodicity was perceived less clearly in interleaved than in seamless sequences. While decreased for interleaved sequences, the consistency of the tapping rhythm was similar for seamless sequences and control sequences that contained a clear physical cue in the signal.

At the neural level, an increase in sustained response emerged after effective periodicity onset and appeared to be modulated by the type of periodicity of a sequence. Previous studies had reported such an increase in sustained activity for tone pip sequences (Barascud et al., 2016), noise-like acoustic patterns (Herrmann & Johnsrude, 2018), and periodic noise (Keceli et al., 2012) with a similar latency (i.e., around half a cycle after effective regularity onset). Functionally, the sustained response was associated with the automatic detection of regularities in acoustic sequences (Barascud et al., 2016; Herrmann & Johnsrude, 2018; Keceli et al., 2012).

When zooming into single cycles, periodicity-related ERPs, which were the focus of our study, were elicited time-locked to the onset of the periodically recurring noise pattern. Over the course of a sequence, this resulted in a pattern of cyclic ERP activity. A prominent frontocentral negativity was elicited between 150 and 400 ms (relative to cycle onset) in the interleaved condition and preceded by an earlier frontal positivity. Several earlier studies reported periodicity-related negative deflections at a similar latency, sometimes preceded by an early positivity, while participants listened to interleaved noise sequences (Andrillon et al., 2015; Berti et al., 2000; Kaernbach et al., 1998) or tone pip sequences (Hodapp & Grimm, 2021). Consistent with previous findings, the frontocentral topography is suggestive of an origin in auditory cortex (Andrillon et al., 2015; Berti et al., 2000; Kaernbach et al., 1998). In the seamless condition, the negativity was weaker and occurred about 50 ms earlier without a preceding positivity, which may point toward a broader negativity with a reduced amplitude as a result of time jitter (within or between listeners, or both). Note that the presence or absence of the early positivity is difficult to interpret due to baseline shifts between conditions and may actually reflect part of the

synchronized response to the periodicity rather than an independent ERP component that is only evoked in the interleaved condition. Andrillon et al. (2015) did not find any periodicity-related ERPs for seamless noise sequences (“diffuse condition” in their terminology). They argued that the ERPs in this condition were leveled out as a consequence of time jitter between listeners because each listener relied on a different idiosyncratic feature to segment the sequence (Andrillon et al., 2015). It is important to note that in the current study not all four specific noise patterns elicited ERPs relative to cycle onset in the seamless condition. This finding is in line with the results of earlier studies, which showed that specific noise patterns differ with regard to how well periodicity is detected by listeners (Agus et al., 2010; Kaernbach, 1993). Although group-level ERPs do not allow to draw clear conclusions with respect to variation within and between subjects, the fact that some noise patterns (mainly pattern 3; pattern 1 to a lesser extent) did evoke a periodicity-related negativity suggests a substantial consistency both within and across participants at least for these patterns. They may contain characteristic features that were used for perceptual segmentation across listeners. Yet, even for these patterns the amplitude of the periodicity-related negativity was reduced in the seamless compared with the interleaved condition. To shed light on whether this difference could be solely explained by temporal variability between, but not within participants, as put forward previously (Andrillon et al., 2015), we compared phase coherence of oscillatory activity separately at the within- and at the between-subject level.

4.2 | Within- and between-subject consistency of perceptual segmentation in periodic noise

Periodic (compared with random) sequences induced consistency of perceptual segmentation both at the within- and the between-subject level. This was reflected behaviourally in the tapping phase coherence and neurally in the phase coherence of oscillatory brain activity at the frequency of the periodicity in the stimulation. Critically, the consistency of neural markers for perceptual segmentation appeared to be stronger for interleaved compared with seamless sequences both within and between listeners.

The increase of within-subject ITPC of the oscillatory activity at the frequency of the stimulation for periodic sequences is in keeping with earlier reports of increased phase coherence of low-frequency neural oscillations for periodic compared with random noise (Andrillon et al., 2015; Luo et al., 2013). Increased phase coherence of

oscillatory activity at the stimulation frequency was previously shown for noise-like acoustic patterns (Herrmann & Johnsrude, 2018). Thus, brain responses seemed to align with the rhythmic recurrence of a particular acoustic feature within a periodic noise sequence. However, contrary to our expectations, ITPC was weaker in the seamless compared with the interleaved condition, which suggested that an individual may not consistently use the same feature to segment a seamless sequence across presentations of the same sequence. This finding may partly be explained by the different length of the repeating segment in seamless and interleaved sequences. The increased length of the repeating segment in the seamless condition, along with the distribution of potential features over a longer period of time, can result in decreased consistency across trials, which in turn leads to diminished ERP amplitudes on average (see above). Moreover, the difference in consistency might also result from the fact that only in the interleaved condition the onsets of the repeating segment are preceded by a portion of novel random noise in every cycle. Further research may disentangle these two aspects by manipulating the length of the repeating segment and the fine structure of the noise sequence independently.

Unlike the EEG data, the behavioral data did not show a difference in within-subject coherence between seamless and interleaved sequences. Tapping phase coherence did not differ significantly between the two periodic conditions, indicating that participants tapped similarly coherently to both types of sequences. This discrepancy between neural and behavioral data may be explained by the different nature of the measures: The tapping phase coherence as a behavioral measure is coarser and might be subject to confounding effects beyond the consistency of perceptual segmentation. For instance, effects of being more consistent in perceptual segmentation but also less confident due to the weaker percept of periodicity in the interleaved condition could counteract and eventually cancel out at the behavioral level. However, it is important to note that (behavioral) consistency was significantly reduced for both seamless and interleaved sequences in comparison with control sequences that contained physical cues for segmentation. This suggests that perceptual segmentation of periodic noise sequences goes along with some variability from trial to trial within one listener and that the amount of variability may be modulated by the type of periodicity. Nevertheless, the fact that there is a substantial consistency across trials indicates that participants did not just motorically learn to tap in a 2-Hz rhythm, but in fact aligned their tapping with acoustic features in the stimulus.

We did not find a significant correlation between ITPC and tapping phase coherence in either periodic condition. Potential reasons for the lack of a significant relationship

may lie in confounding effects, in particular on the behavioral measure, that may also account for the lack of a statistically significant difference in tapping phase coherence between the two periodic conditions (see above). It may be plausible to assume that many more factors than the consistency of perceptual segmentation alone affect tapping behavior along various processing steps from periodicity perception to motor planning. More generally, brain-behavior correlations (or the absence thereof) should be interpreted with caution in samples in the size of ours, as they may lack statistical power to reliably detect (small) correlations between neural and behavioral measures.

As expected, between-subject ISPC was increased in the interleaved compared with the seamless condition. This difference in consistency between the two types of periodic sequences may again be explained by the length of the repeating segment and the fine-structure of the sequences. As outlined above for the within-subject consistency and in accordance with the argumentation by Andrillon et al. (2015), the shorter duration of the repeating segment that always followed a portion of unfamiliar random noise may have reduced the temporal jitter and increased consistency of perceptual segmentation between individuals. Albeit to a lesser extent, seamless sequences also induced consistency between listeners. However, we again observed differences between specific noise patterns for seamless sequences. Specifically, two of the four patterns appeared to drive the effect in this condition. This finding suggests that, at least for some noise patterns, listeners use subtle features that are shared between individuals to perceptually segment the noise sequence. Although the difference between interleaved and seamless sequences supports the idea that participants rely on short, temporally local features, the increased ISPC for single patterns in the seamless condition indicates that these features may not necessarily be idiosyncratic. Which critical spectrotemporal properties might be preferentially used for consistent perceptual segmentation (within and between individuals) remains an outstanding question for future investigation.

5 | CONCLUSIONS

The present study aimed to advance the understanding of mechanisms that underlie perceptual segmentation of unstructured and unfamiliar auditory input. To the best of our knowledge, this was the first study to systematically analyze consistency of perceptual segmentation separately within and between individuals. This approach allowed us to disentangle variation at these two levels, which were usually confounded in the group-level averages analyzed in previous studies. In short, although

seamless sequences induced a stronger percept of periodicity, interleaved sequences were associated with a stronger consistency of perceptual segmentation both within and between listeners. While earlier studies had assumed that the difference between seamless and interleaved noise with regard to periodicity-related brain responses at the group level can be merely explained by differences in between-subject variability, here we showed that also differences in within-subject (inter-trial) variability play a role. Thus, the amount of temporal jitter was increased not only between, but also within listeners for seamless relative to interleaved sequences, which may overall point toward a less consistent use of exactly one characteristic feature per noise pattern than claimed previously. In particular for seamless sequences, consistency between participants depended on the specific noise pattern, such that some sequences were segmented more consistently than others. These results are in line with the assumption that listeners rely on subtle local features that are learned through repeated exposure to perceptually segment periodic noise sequences. However, differences between specific noise patterns with regard to between-subject consistency challenge the assumption that those features are necessarily idiosyncratic in nature. Instead, the present findings rather suggest that a preference for certain spectral features (which remain to be specified by future research) might be shared between individuals.

AUTHOR CONTRIBUTIONS

Hanna Ringer: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Erich Schröger:** Conceptualization; supervision; writing – review and editing. **Sabine Grimm:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; supervision; visualization; writing – review and editing.

ACKNOWLEDGEMENT

The authors thank Andreas Widmann for methodological advice, Marc Pabst for help with EEG data collection, and János Horváth and Wolfgang Löhrmann for assistance with building the tapping device. The study was funded by the German Research Foundation (www.dfg.de) with the project number GR3412/2-2. Data processing procedures and confirmatory statistical analyses were preregistered at osf.io/ju2vh prior to analysis of the data. The results reported here were previously reported in an unpublished M.Sc. thesis by Hanna Ringer, submitted at Leipzig University in August 2020, and presented in a talk at the 20th World Congress of Psychophysiology (IOP2021) in September 2021.

CONFLICTS OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Hanna Ringer  <https://orcid.org/0000-0001-6115-7878>

Erich Schröger  <https://orcid.org/0000-0002-8321-6629>

Sabine Grimm  <https://orcid.org/0000-0002-9071-5944>

REFERENCES

- Agus, T. R., & Pressnitzer, D. (2013). The detection of repetitions in noise before and after perceptual learning. *The Journal of the Acoustical Society of America*, *134*(1), 464–473. <https://doi.org/10.1121/1.4807641>
- Agus, T. R., Thorpe, S. J., & Pressnitzer, D. (2010). Rapid formation of robust auditory memories: Insights from noise. *Neuron*, *66*(4), 610–618. <https://doi.org/10.1016/j.neuron.2010.04.014>
- Andrillon, T., Kouider, S., Agus, T., & Pressnitzer, D. (2015). Perceptual learning of acoustic noise generates memory-evoked potentials. *Current Biology*, *25*(21), 2823–2829. <https://doi.org/10.1016/j.cub.2015.09.027>
- Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. *Brain and Cognition*, *48*(1), 66–79. <https://doi.org/10.1006/brcg.2001.1304>
- Barascud, N., Pearce, M. T., Griffiths, T. D., Friston, K. J., & Chait, M. (2016). Brain responses in humans reveal ideal observer-like sensitivity to complex acoustic patterns. *Proceedings of the National Academy of Sciences*, *113*(5), E616–E625. <https://doi.org/10.1073/pnas.1508523113>
- Bendixen, A. (2014). Predictability effects in auditory scene analysis: A review. *Frontiers in Neuroscience*, *8*(8), 1–16. <https://doi.org/10.3389/fnins.2014.00060>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate. *Journal of the Royal Statistical Society: Series B*, *57*(1), 289–300. <https://doi.org/10.1017/CBO9781107415324.004>
- Berti, S., Schröger, E., & Mecklinger, A. (2000). Attentive and pre-attentive periodicity analysis in auditory memory: An event-related brain potential study. *Neuroreport*, *11*(9), 1883–1887. <https://doi.org/10.1097/00001756-200006260-00016>
- Bianco, R., Harrison, P. M., Hu, M., Bolger, C., Picken, S., Pearce, M. T., & Chait, M. (2020). Long-term implicit memory for sequential auditory patterns in humans. *eLife*, *9*, e56073. <https://doi.org/10.7554/eLife.56073>
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Bregman, A. S. (1990). *Auditory scene analysis: The perceptual organization of sound*. MIT Press.
- Chait, M. (2020). How the brain discovers structure in sound sequences. *Acoustical Science and Technology*, *41*(1), 48–53. <https://doi.org/10.1250/ast.41.48>
- Cohen, M. A., Horowitz, T. S., & Wolfe, J. M. (2009). Auditory recognition memory is inferior to visual recognition memory. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(12), 4947–4952. <https://doi.org/10.1073/pnas.0810001106>

- States of America*, 106(14), 6008–6010. <https://doi.org/10.1073/pnas.0811884106>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Gibson, E. J. (1969). *Principles of perceptual learning and development*. Appleton-Century-Crofts.
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, 31(5), 681–697. [https://doi.org/10.1016/S0896-6273\(01\)00424-X](https://doi.org/10.1016/S0896-6273(01)00424-X)
- Guttman, N., & Julesz, B. (1963). Lower limits of auditory periodicity analysis. *The Journal of the Acoustical Society of America*, 35(4), 610. <https://doi.org/10.1121/1.1918551>
- Hautus, M. J., & Lee, A. (2006). Estimating sensitivity and bias in a yes/no task. *British Journal of Mathematical and Statistical Psychology*, 59(2), 257–273. <https://doi.org/10.1348/000711005X65753>
- Henry, M. J., & Herrmann, B. (2014). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing & Time Perception*, 2(1), 62–86. <https://doi.org/10.1163/22134468-00002011>
- Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proceedings of the National Academy of Sciences*, 109(49), 20095–20100. <https://doi.org/10.1073/pnas.1213390109>
- Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *The Journal of Neuroscience*, 38(24), 5466–5477. <https://doi.org/10.1523/JNEUROSCI.0346-18.2018>
- Hodapp, A., & Grimm, S. (2021). Neural signatures of temporal regularity and recurring patterns in random tonal sound sequences. *European Journal of Neuroscience*, 53(8), 2740–2754. <https://doi.org/10.1111/ejn.15123>
- Kaernbach, C. (1992). On the consistency of tapping to repeated noise. *The Journal of the Acoustical Society of America*, 92(2), 788–793. <https://doi.org/10.1121/1.403948>
- Kaernbach, C. (1993). Temporal and spectral basis of the features perceived in repeated noise. *The Journal of the Acoustical Society of America*, 94(1), 91–97. <https://doi.org/10.1121/1.406946>
- Kaernbach, C. (2004). The memory of noise. *Experimental Psychology*, 51(4), 240–248. <https://doi.org/10.1027/1618-3169.51.4.240>
- Kaernbach, C., Schröger, E., & Gunter, T. C. (1998). Human event-related brain potentials to auditory periodic noise stimuli. *Neuroscience Letters*, 242(1), 17–20. [https://doi.org/10.1016/S0304-3940\(98\)00034-2](https://doi.org/10.1016/S0304-3940(98)00034-2)
- Kang, H., Agus, T. R., & Pressnitzer, D. (2017). Auditory memory for random time patterns. *The Journal of the Acoustical Society of America*, 142(4), 2219–2232. <https://doi.org/10.1121/1.5007730>
- Keceli, S., Inui, K., Okamoto, H., Otsuru, N., & Kakigi, R. (2012). Auditory sustained field responses to periodic noise. *BMC Neuroscience*, 13(1), 7. <https://doi.org/10.1186/1471-2202-13-7>
- Kleiner, M., Brainard, D., Pelli, D. G., Ingling, A., Murray, R., & Broussard, C. (2007). “What’s new in Psychtoolbox-3?”. Perception 36 ECVF Abstract Supplement.
- Kumar, S., Bonnici, H. M., Teki, S., Agus, T. R., Pressnitzer, D., Maguire, E. A., & Griffiths, T. D. (2014). Representations of specific acoustic patterns in the auditory cortex and hippocampus. *Proceedings of the Royal Society B: Biological Sciences*, 281(1791), 20141000. <https://doi.org/10.1098/rspb.2014.1000>
- Lawrence, M. A. (2016). ez: Easy analysis and visualization of factorial experiments. R package version 4.4-0. <https://CRAN.Rproject.org/package=ez>
- Limbert, C., & Patterson, R. D. (1982). Tapping to repeated noise. *The Journal of the Acoustical Society of America*, 71(S1), S38. <https://doi.org/10.1121/1.2019365>
- Luo, H., Tian, X., Song, K., Zhou, K., & Poeppel, D. (2013). Neural response phase tracks how listeners learn new acoustic representations. *Current Biology*, 23(11), 968–974. <https://doi.org/10.1016/j.cub.2013.04.031>
- Macmillan, N. A. (2001). Signal detection theory. In N. J. Smelser & P. B. Baltes (Eds.), *International Encyclopedia of the social & behavioral sciences* (pp. 14075–14078). Pergamon: Oxford. <https://doi.org/10.1016/b0-08-043076-7/00677-x>
- Maravall, M., Ostojic, S., Pressnitzer, D., & Chait, M. (2018). More than the sum of its parts: Perception and neuronal underpinnings of sequence processing. *Neuroscience*, 389, 1–3. <https://doi.org/10.1016/j.neuroscience.2018.07.043>
- Maris, E. (2012). Statistical testing in electrophysiological studies. *Psychophysiology*, 49(4), 549–565. <https://doi.org/10.1111/j.1469-8986.2011.01320.x>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- McDermott, J. H., Schemitsch, M., & Simoncelli, E. P. (2013). Summary statistics in auditory perception. *Nature Neuroscience*, 16(4), 493–498. <https://doi.org/10.1038/nn.3347>
- Nelken, I., Bizley, J., Shamma, S. A., & Wang, X. (2014). Auditory cortical processing in real-world listening: The auditory system going real. *Journal of Neuroscience*, 34(46), 15135–15138. <https://doi.org/10.1523/JNEUROSCI.2989-14.2014>
- Oldfield, R. C. (1971). The Edinburgh handedness inventory. *Neuropsychologia*, 9, 97–111. <https://doi.org/10.1002/mus.10529>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 1–9. <https://doi.org/10.1155/2011/156869>
- Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage*, 198, 181–197. <https://doi.org/10.1016/j.neuroimage.2019.05.026>
- Rajendran, V. G., Harper, N. S., Abdel-Latif, K. H. A., & Schnupp, J. W. H. (2016). Rhythm facilitates the detection of repeating sound patterns. *Frontiers in Neuroscience*, 10, 1–7. <https://doi.org/10.3389/fnins.2016.00009>
- Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, 12(6), 969–992. <https://doi.org/10.3758/BF03206433>
- Repp, B. H., & Su, Y.-H. (2013). Sensorimotor synchronization: A review of recent research (2006–2012). *Psychonomic Bulletin & Review*, 20(3), 403–452. <https://doi.org/10.3758/s13423-012-0371-2>
- Southwell, R., Baumann, A., Gal, C., Barascud, N., Friston, K., & Chait, M. (2017). Is predictability salient? A study of attentional capture by auditory patterns. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1714), 20160105. <https://doi.org/10.1098/rstb.2016.0105>
- Southwell, R., & Chait, M. (2018). Enhanced deviant responses in patterned relative to random sound sequences. *Cortex*, 109, 92–103. <https://doi.org/10.1016/j.cortex.2018.08.032>

- Viswanathan, J., Rémy, F., Bacon-Macé, N., & Thorpe, S. J. (2016). Long term memory for noise: Evidence of robust encoding of very short temporal acoustic patterns. *Frontiers in Neuroscience, 10*, 1–11. <https://doi.org/10.3389/fnins.2016.00490>
- Winkler, I., Denham, S. L., & Nelken, I. (2009). Modeling the auditory scene: Predictive regularity representations and perceptual objects. *Trends in Cognitive Sciences, 13*(12), 532–540. <https://doi.org/10.1016/j.tics.2009.09.003>

How to cite this article: Ringer, H., Schröger, E., & Grimm, S. (2022). Within- and between-subject consistency of perceptual segmentation in periodic noise: A combined behavioral tapping and EEG study. *Psychophysiology, 00*, e14174. <https://doi.org/10.1111/psyp.14174>