

# Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity

Massimo Lumaca<sup>1,2</sup>  | Niels Trusbak Haumann<sup>1</sup> | Elvira Brattico<sup>1</sup> | Manon Grube<sup>1</sup> | Peter Vuust<sup>1</sup>

<sup>1</sup>Department of Clinical Medicine, Center for Music in the Brain, Aarhus University & The Royal Academy of Music, Aarhus C, Denmark

<sup>2</sup>SISSA International School for Advanced Studies, Trieste, Italy

## Correspondence

Massimo Lumaca, Department of Clinical Medicine, Center for Music in the Brain, Aarhus University & The Royal Academy of Music, Aarhus C, Denmark.  
Email: massimo.lumaca@clin.au.dk

## Funding information

Danmarks Grundforskningsfond, Grant/Award Number: DNR117

## Abstract

The human brain's ability to extract and encode temporal regularities and to predict the timing of upcoming events is critical for music and speech perception. This work addresses how these mechanisms deal with different levels of temporal complexity, here the number of distinct durations in rhythmic patterns. We use electroencephalography (EEG) to relate the mismatch negativity (MMN), a proxy of neural prediction error, to a measure of information content of rhythmic sequences, the Shannon entropy. Within each of three conditions, participants listened to repeatedly presented standard rhythms of five tones (four inter-onset intervals) and of a given level of entropy: zero (isochronous), medium entropy (two distinct interval durations), or high entropy (four distinct interval durations). Occasionally, the fourth tone was moved forward in time that it occurred 100 ms (small deviation) or 300 ms early (large deviation). According to the predictive coding framework, high-entropy stimuli are more difficult to model for the brain, resulting in less confident predictions and yielding smaller prediction errors for deviant sounds. Our results support this hypothesis, showing a gradual decrease in MMN amplitude as a function of entropy, but only for small timing deviants. For large timing deviants, in contrast, a modulation of activity in the opposite direction was observed for the earlier N1 component, known to also be sensitive to sudden changes in directed attention. Our results suggest the existence of a fine-grained neural mechanism that weights neural prediction error to the complexity of rhythms and that mostly manifests in the absence of directed attention.

## KEYWORDS

EEG, MMN, predictive coding, rhythmic complexity, Shannon entropy

## 1 | INTRODUCTION

The processing of fast temporal patterns, such as rhythms of music and speech, is in part grounded in prediction. It relies

**Abbreviations:** ANOVA, analysis of variance; EEG, electroencephalography; ERP, event-related potentials; IOI, inter-onset interval; ISI, interstimulus interval; LME, linear mixed-effects model; MMN, mismatch negativity; SD, standard deviation.

Edited by Guillaume Rousselet. Reviewed by Robin Ince.

All peer review communications can be found with the online version of the article.

upon the listener's ability to extract regularities from complex acoustic streams and develop temporal expectancies about upcoming events (Bendixen, SanMiguel, & Schröger, 2012; Wacongne, Changeux, & Dehaene, 2012). Therefore, rhythm perception has been suggested to be a Bayesian process (Elliott, Wing, & Welchman, 2014) consistent with the framework of predictive coding (Friston, 2002, 2005). As a rhythm unfolds, the listener's brain automatically tracks temporal regularities to generate a probabilistic model, in order to predict *what* might most likely be encountered next,

and *when* (Winkler, Denham, & Nelken, 2009). The brain's goal is to minimize the discrepancy ("error") between its internal model and the sensory input, in order to attain temporally precise predictions. In the event of a mismatch between the brain's predictive model and the sensory input, an error signal is generated, which seems to be reflected in a pre-attentively generated auditory-evoked potential, the mismatch negativity response (MMN; Näätänen, Gaillard, & Mäntysalo, 1978).

Previous MMN research has demonstrated the remarkable abilities of the auditory system to encode sound features and to extract complex relations in sound patterns. An MMN is evoked after "oddball" changes in the spatial (i.e. location), spectral (loudness, frequency, or timbre) or temporal (durations, or inter-onset interval) dimension of repeated sounds (Näätänen, Paavilainen, Rinne, & Alho, 2007). Such changes also modulate the activity of an earlier component called N1, which typically occurs 100 ms post-onset of any sound (Näätänen & Picton, 1987). However, of these two components, only the MMN is sensitive to violations of extracted, statistical regularities in stimuli. The N1, in contrast, appears to reflect the detection of feature-specific deviations. Thus, only the MMN can be interpreted as a neural signature of error processing, and its elicitation be taken as evidence that a regularity was extracted from the input (Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009; Vuust & Witek, 2014). To date, it remains unclear how far the extraction of temporal regularities and the timing accuracy (or "precision") of the internal predictive model are affected by stimulus information content (or complexity), here the number of distinct inter-onset intervals (IOIs) within a rhythmic pattern.

Auditory rhythms can be formalized mathematically as a series of IOIs (Cohen, 1962; Ravnani & Madison, 2017; Toussaint, 2013). A metric derived from information theory, the Shannon entropy (Shannon, 1948), summarizes this information by a single value, measured in bits. This quantity can be applied to express the amount of complexity in a rhythm. It takes its maximum value for patterns where all interval durations are different and the succession of events is difficult to model predictively. Conversely, entropy is minimal (i.e. zero) for isochronous patterns, where all intervals have the same duration and all events are fully predictable in time. We test here the hypothesis that the entropy of rhythms is likely to affect the efficiency of extracting and encoding regularities, as both those processes are constrained by the brain's capacities to integrate, store and analyse information over time. Therefore, we here investigate whether and how rhythmic complexity affects the precision of the internal predictive model.

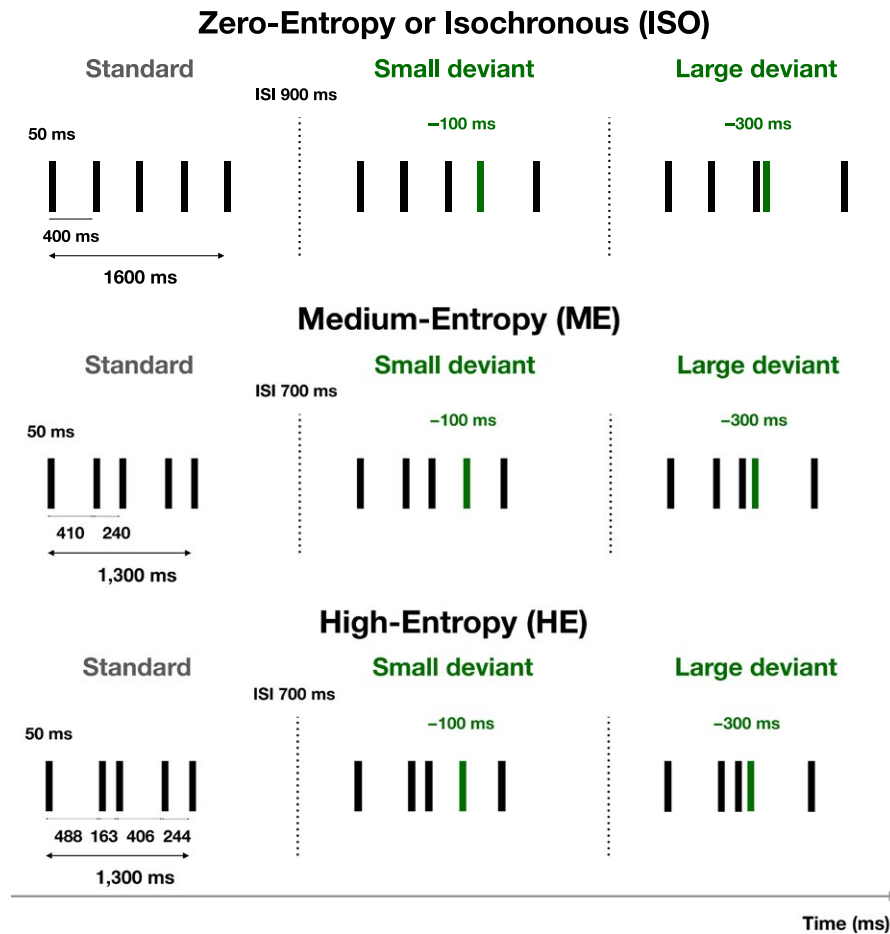
One key assumption of predictive coding is that the brain not only forms a predictive model of future events but also

estimates its reliability (Feldman & Friston, 2010; Rao, 2005). In weaker models, reliability is low and responses to unexpected events are down-weighted. In other words, the less reliable or precise the brain's estimate for an internal model is, the smaller the neural response will be to deviations from that model. Following this, we expect a progressive decrease in the prediction error with increasing complexity (or entropy) of rhythms.

Previous oddball studies have reported a decreased neural response to randomly timed compared to isochronous stimuli (Costa-Faidella, Baldeweg, Grimm, & Escera, 2011; see also Schwartz, Farrugia, & Kotz, 2013; Tavano, Widmann, Bendixen, Trujillo-Barreto, & Schröger, 2014). However, these two conditions represent only the two end points of a continuous spectrum of temporal predictability (Paavilainen, 2013). How the mismatch signal is modulated by different degrees of temporal uncertainty remains to be investigated. In addition, the decrease of neural response observed for random sequences (either in pitch or temporal dimension) has mainly been attributed to repetition suppression (Ewbank et al., 2011; May et al., 1999; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). It is commonly observed that responses to repeated standard sounds decrease over time more for regular than for random sequences, while deviant responses remain constant for both (Arnal & Giraud, 2012; Knolle, Schröger, Baess, & Kotz, 2012). Thus, the relative increase in positivity of standard responses for regular sequences might largely or even solely account for larger MMNs observed for those, leaving the contribution of deviant-evoked activity unclear (see Southwell & Chait, 2018, for a N1 account).

This study addresses these questions with EEG, by applying an entropic metric (Shannon, 1948) within an oddball paradigm experiment that tests MMN amplitude as a function of rhythmic complexity and magnitude of deviation. The entropy of five-tone rhythms (i.e. four time intervals) was varied parametrically across three separate runs: from 0 (isochronous) to 1 (medium entropy: two distinct durations) to 2 (high entropy: four distinct durations; Figure 1). Small deviations were designed to produce a weak, barely noticeable change in rhythmic timing; large deviations were meant to induce a salient change in the grouping of tones, or "rhythmic contour".

We hypothesized that with increasing stimulus entropy, the brain's predictive model would become less accurate, and therefore less sensitive to small deviations in timing. Accordingly, we expected a down-weighted prediction error, reflected in a decrease in MMN for small timing deviations in rhythmic patterns of increasing entropy. For large timing deviations, in contrast, we expected the change to be salient enough to produce deviance detection across all three conditions, resulting in a similarly sized MMN, independent of the entropy level.



**FIGURE 1** Schematic illustration of stimuli and paradigm. The top panel displays the zero entropy or isochronous condition (ISO), in which standard sequences consist of five identical tones equally spaced (400 ms apart). The middle and bottom panels display the medium-entropy (ME) and high-entropy conditions (HE), in which five-tone sequences are composed of time intervals of two (ME, 410 and 240 ms) and four (HE, 488, 163, 406 and 244 ms) distinct durations respectively. In all conditions, the deviant stimuli (in green) feature an earlier presentation of the fourth tone by 100 ms (small deviant) or 300 ms (large deviant) compared to its standard position

## 2 | METHODS

### 2.1 | Participants

Seventeen right-handed volunteers (11 females) participated in the study (mean age 25.9; *SD* 5.6; range 20–39 years old; five other participants were excluded due to excessive artefacts). All participants were students at the Norwegian University of Science and Technology (NTNU) with no formal musical training beyond school education. No participants reported any neurological dysfunction or a hearing deficit at the time of testing. All participants gave their written informed consent and received monetary compensation. The neurophysiological data used here were acquired as a part of another project approved by the Ethics Committee at the International School for Advanced Studies (SISSA) and by the Norwegian Social Science Data Services (NSD project 47526; Lumaca, Haumann,

Vuust, Brattico, & Baggio, 2018). Experimental procedures were entirely in accord with the relevant guidelines and regulations.

### 2.2 | Procedure

Each participant completed an EEG session of three runs (1 per condition), during which standard rhythms were presented at three different levels of complexity (isochronous, 0 bit; medium entropy, 1 bit; and high entropy, 2 bits). Participants were seated in a sound-attenuated booth and asked to ignore the sounds while watching a silent subtitled movie (centred on the screen). Within each run, sine-wave equitone standard rhythms of five tones were presented repeatedly (80%), interspersed with *small* (10%) and *large* (10%) deviants, in which the fourth tone appeared early compared to its standard position (Figure 1). Each run was divided into four blocks of 100 stimuli, amounting to

a total of 1,200 stimuli per condition (960 standards, 240 deviants). One run took 15 min for the isochronous condition and 13.3 min for the medium- and high-entropy conditions, respectively, with short breaks in between, resulting in around 1 hr recording time. The order of conditions was randomized and balanced across subjects.

## 2.3 | Stimuli

Figure 1 illustrates standard and deviant stimuli used in each condition, all composed of five 50 ms sinusoidal tones (5 ms rise and fall). Stimulus complexity was calculated by applying the Shannon entropy (Shannon, 1948) to the series of IOIs, using the following equation:

$$H(X) = - \sum p(x_i) \log_2 p(x_i),$$

where  $X$  is the vector of IOIs in a sequence and  $p(x_i)$  is the probability that the element  $i$  occurs in that sequence (given the alphabet of the elements and their relative frequency). Thus, the Shannon entropy is 0 bit for isochronous standard stimuli (400 ms IOIs), 1 bit for medium-entropy stimuli (IOIs: 410, 240, 410 and 240 ms) and 2 bits for high-entropy stimuli (IOIs: 488, 163, 406 and 244 ms). Stimuli in the high- and medium-entropy conditions were 1,300 ms long and presented with a 700 ms interstimulus interval (ISI; the silent interval between the offset of one sequence's tone and the onset of the next). Isochronous stimuli were 1,600 ms long (IOIs: 400, 400, 400 and 400 ms) with an ISI of 900 ms. The longer duration of isochronous stimuli was necessary to have IOIs sufficiently long (i.e. >300 ms) to produce large timing deviants. Given the longer duration, we chose for isochronous stimuli also a proportionally longer ISI. In small deviants (10%), the fourth tone was shifted 100 ms earlier and followed the third tone by 300 ms. In large deviants (10%), the fourth tone was shifted 300 ms earlier, following the third tone by 100 ms. Notice that only the large deviants violate the rhythmic "contour", or grouping of tones (Monahan, 1985). The order of standard and deviant stimuli was randomized, with the only constraint that at least one standard pattern appeared before every deviant pattern. To reduce N1 refractoriness effects to isochronous patterns (Costa-Faidella et al., 2011), the equitone rhythms were randomly roved in frequency (315, 397 and 500 Hz).

## 2.4 | EEG recording and processing

Ag/AgCL electrodes were mounted in an EEG actiCap (Brain Products), following the international 10–20 system. EEG was recorded from 64 scalp sites with a sampling rate of 1,000 Hz and an online reference at FCz. Offline data were down-sampled to 500 Hz, bandpass-filtered

(0.1–30 Hz; roll-off = 12 dB/octave), re-referenced to the averaged mastoid electrodes and epoched (–100 to 600 ms from fourth tone onset), using the Matlab toolboxes ERPlab (Lopez-Calderon & Luck, 2014) and EEGLab (Delorme & Makeig, 2004). Then, epochs were scanned by an automatic artefact-detection algorithm (peak-to-peak; moving window = 200 ms). Epochs exceeding  $\pm 70 \mu\text{V}$  at any EEG channel were considered artefacts and rejected. Valid epochs were averaged by stimulus type (standard, small and large deviant) and deviant minus standard difference waves were then computed per participant and baseline corrected by a pre-stimulus interval (–100 to 0 ms).

## 2.5 | Mass univariate analyses of ERP data

The aim was to examine the effect of increasing rhythmic complexity on MMN amplitude. For this purpose, we adopted a mass univariate approach with a permutation statistic method to correct for multiple comparisons (Groppe, Urbach, & Kutas, 2011a, 2011b). The analysis was implemented using the Factorial Mass Univariate ERP toolbox (Fields, 2017) in EEGLab. Specifically, we first computed an ANOVA for every electrode (64) and time points of interest (details below). Second, we assessed statistical significance by a non-parametric permutation test based on the  $F_{\text{max}}$  statistic (Blair & Karniski, 1993). In  $F_{\text{max}}$  permutation testing, a null distribution is constructed by repeatedly sampling the data types from the ERP data, and selecting the largest  $F$ -value for each comparison ( $F_{\text{max}}$ ).  $F$ -values exceeding the  $1-\alpha$  percentile of the  $F_{\text{max}}$  null distribution are deemed significant. This method provides a rigorous control of the family-wise error rate. In all analyses, we set the number of permutations per comparison to 10,000 and the family-wise alpha to 0.05. To limit the number of comparisons, increase statistical power and avoid spurious effects, ERPs were further down-sampled to 125 Hz, and analysed only in the MMN time window (50–250 ms post-onset; Luck, 2014). A total number of 1,664 comparisons were performed (64 electrodes  $\times$  26 time points).

In the first analysis, we tested for the presence of an MMN separately for small and large deviants. A two-way ANOVA was performed at all 64 electrodes and 26 time points. We used Stimulus Type (standard, deviant) and Entropy (zero, medium, high) as within-subject factors, and ERP amplitude as the dependent variable. In the second analysis, we carried out a one-way ANOVA to test the effect of entropy on MMN amplitude. In this analysis, we used entropy as a within-subject factor and ERP amplitude of deviant minus standard difference waves as the dependent variable. For both analyses, we performed permutation-corrected post hoc comparisons (i.e. one-way ANOVAs) for those factors that yielded significant main effects or interactions.

## 2.6 | Linear mixed-effect model (LME) analysis

To examine whether the entropy of rhythms has a significant effect on MMN amplitude, we fitted linear mixed-effect models using R (R Core Team, 2014) and the *lme4* package (Bates, Maechler, & Bolker, 2012). The participants were entered as the “by-subject” random effect, the rhythmic entropy as the fixed effect and the individual's deviant minus standard MMN amplitude as the dependent variable. A separate LME was run for small- and large-deviant responses. In this analysis, we only entered data from one defined time window, large enough to entail an MMN (160–240 ms). *p*-Values were obtained by a likelihood ratio test comparing a full model (with fixed effects and random structure) to a null model (only random structure).

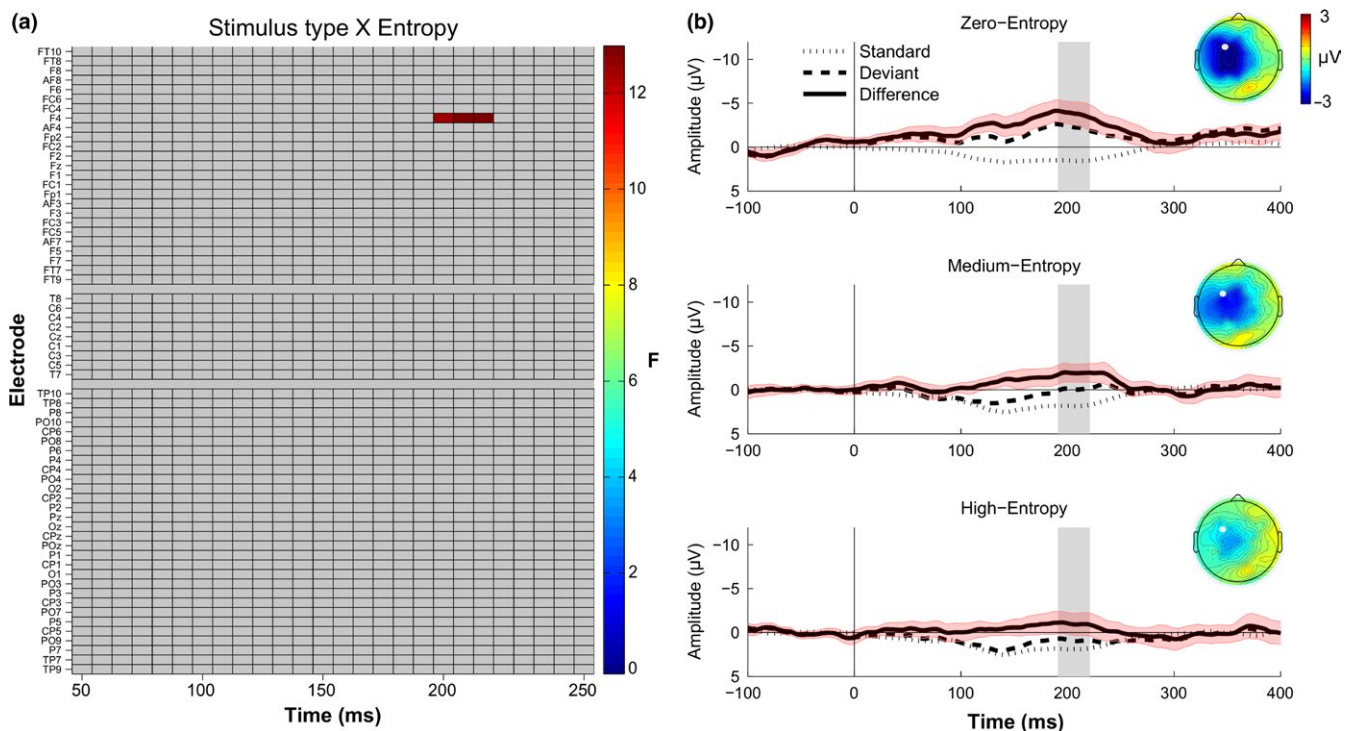
## 3 | RESULTS

Our results, presented in detail below, show that both small and large temporal deviations induce a neural response

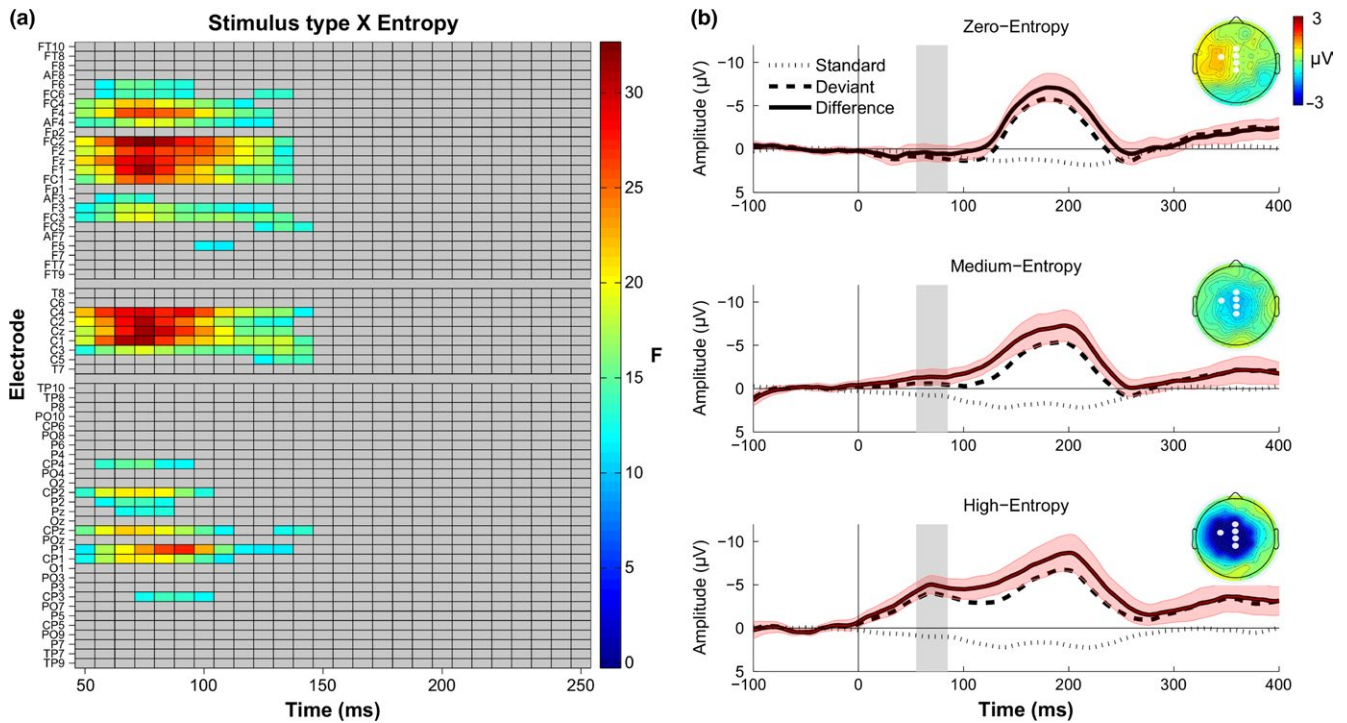
with a time course and topographical distribution typical of MMN. They further demonstrate a significant effect of rhythmic entropy on the amplitude of the ERP response, however, with the time range and direction of modulation differing according to the magnitude of the temporal deviation. Specifically, only for small deviants we observed a linear decrease in the MMN within its well-characterized time window. Conversely, a linear increase in N1 amplitude as a function of entropy was observed in large timing deviants only.

### 3.1 | MMN

Figures 2 and 3 display the main results of the first mass univariate analysis. The deviant response to both timing deviants (small and large) was significantly more negative than that to corresponding standard tones (see Table 1 for omnibus ANOVA results). A post hoc analysis on the main effect of “stimulus type” showed that for all entropy levels, the ERPs evoked by large deviants were significantly more negative than the ERPs for the corresponding standard tones at several



**FIGURE 2** Results for small timing deviant sounds: main interaction between stimulus type and entropy. (a) Raster diagram with red rectangles showing significant differences between *small* timing deviant responses and standard responses across entropy levels according to the *F*max test. The colour bar on the right indicates *F*-values. *F*max values for the main interaction are reported in Table 1. (b) In the trace plot are depicted the grand-average ERPs ( $N = 17$ ), plus the grand-average difference wave, for the electrode showing the main interaction (i.e. F4; see white point in the scalp map) for zero-entropy (top row), medium-entropy (middle row) and high-entropy stimuli (bottom row). The red shaded area on the difference potential marks the 95% confidence interval (CI). On the right of each plot, the relative topographic isovoltage map of grand-average difference waves. Isovoltage maps were produced in a 30 ms time window centred at the time point where the *F* critical values were maximal ( $206 \pm 15$  ms post-onset). This time window is shown as a shaded grey region in the ERP plot. Note that the same time window was used for the MMN time window in Figure 5



**FIGURE 3** Results for large timing deviant sounds: main interaction between stimulus type and entropy. (a) Raster diagram with red rectangles showing significant differences between *large* timing deviant responses and standard responses across entropy levels according to the *F*<sub>max</sub> test. The colour bar on the right indicates *F*-values. *F*<sub>max</sub> values for the main interaction are reported in Table 1. (b) In the trace plot are depicted the grand-average ERPs (*N* = 17), plus the grand-average difference wave, for some of the electrodes showing the main interaction (i.e. C1, Cz, C2, C4 and F2; see white points in the scalp map) for zero-entropy (top row), medium-entropy (middle row) and high-entropy stimuli (bottom row). The red shaded area on the difference potential marks the 95% confidence interval (CI). On the right of each plot, the relative topographic isovoltage map of grand-average difference waves. Isovoltage maps were produced in a 30 ms time window centred at the time point where the *F* critical values were maximal (70 ± 15-ms post-onset). This time window is shown as a shaded grey region in the ERP plot. Note that the same time window was used for the N1 time window in Figure 5

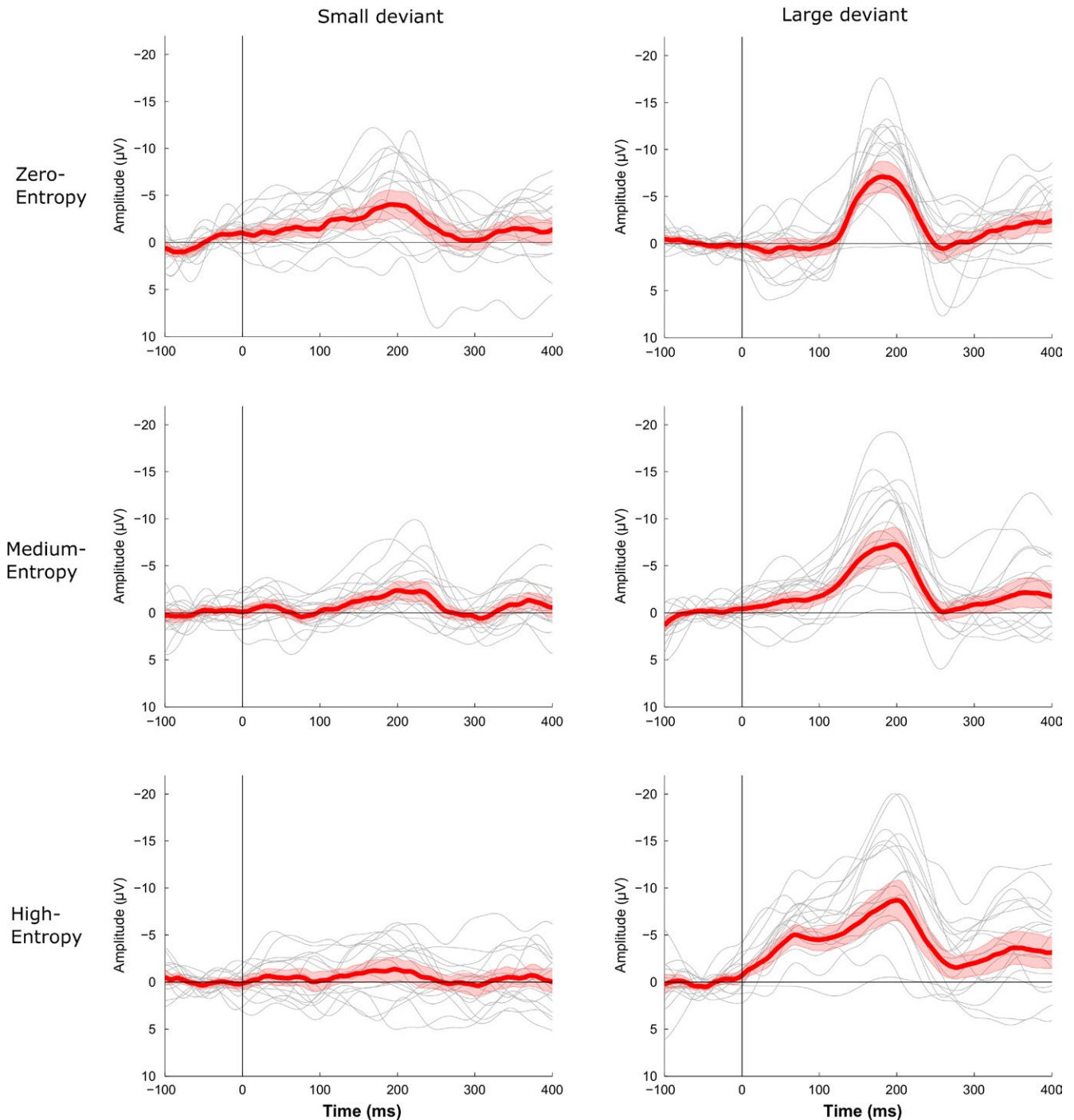
**TABLE 1** Two-way ANOVA on ERP responses to standard and deviant stimuli performed at every electrode and time points of interest (50–250 ms post-onset)

	Small deviant				Large deviant			
	<i>F</i> <sub>max</sub>	<i>df</i>	<i>p</i>	$\eta_p^2$	<i>F</i> <sub>max</sub>	<i>df</i>	<i>p</i>	$\eta_p^2$
Main effect								
Stimulus type	35.76	(1,16)	0.008	0.69	104.86	(1,16)	0.0003	0.86
Entropy	26.55	(2,32)	0.0003	0.62	34.37	(2,32)	0.0001	0.68
Two-way interactions								
Stimulus type × Entropy	12.88	(2,32)	0.03	0.45	32.42	(2,32)	0.0001	0.67

*Note.* Main effects are Stimulus type (standard, deviant) and Entropy (zero, medium, high). Listed in the columns: *F*<sub>max</sub> values, degrees of freedom (*df*), *p*-values and estimates of effect sizes ( $\eta_p^2$ ). Statistical significance was assessed by using a non-parametric permutation test based on *F*<sub>max</sub> statistic.

fronto-central and centro-parietal electrodes (ISO: critical *F*-value: ±23.21, time range: 150–220 ms post-onset; ME: critical *F*-value: ±22.35, time range: 120–220 ms post-onset; HE: critical *F*-value: ±18.48, time range: 50–220 ms post-onset; Supporting Information Figures S1–S3). A similar effect was observed for the MMNs evoked by small deviants, where the deviant minus standard difference was significant

at fronto-central electrodes for zero and medium entropy (ISO: critical *F*-value: ±23.21; ME: critical *F*-value: ±27.05; Supporting Information Figures S4 and S5) but not for high entropy (HE: critical *F*-value: ±24.29; *p* = 0.13). These results suggest that an MMN was elicited in most conditions, whereas no evidence was found for small deviants in the high-entropy condition.



**FIGURE 4** Time course of the deviant minus standard difference ERPs. Individual (grey lines) and grand-average difference waves (red line) ( $N = 17$ ) for small (left) and large timing deviant sounds (right), in zero- (top row), medium- (middle row), and high-entropy stimuli (bottom row). The red shaded area around the grand-average difference potentials marks the 95% confidence interval (CI). The individual waveforms shown here were low-pass filtered using a 1–20 Hz bandpass finite impulse response (FIR) zero-phase filter

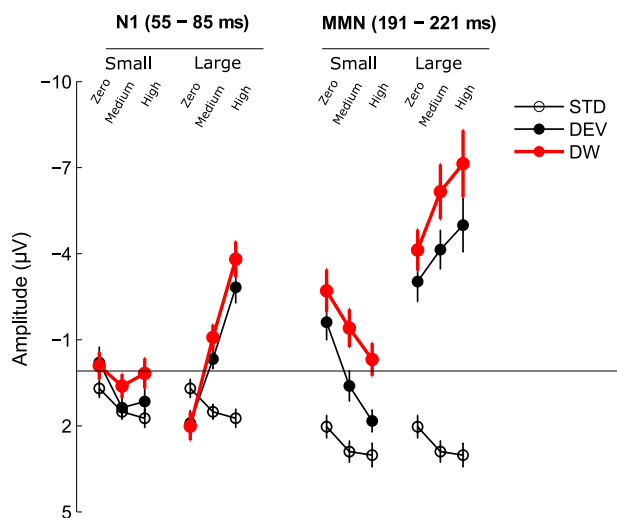
### 3.2 | Modulation of MMN amplitude by rhythmic entropy

Figures 2a and 3a show the ERPs for small and large deviants, respectively, for those electrodes and time points at which the interaction between “entropy” and “stimulus type”

was significant. Our results suggest a modulation of the deviant minus standard ERPs by rhythmic complexity that depends on the magnitude of deviation. One effect was found on small-deviant responses in the MMN window ( $\approx 200$  ms). As illustrated in Figure 2a,b, this modulation presents a significant decrease in the difference waves from zero to high

entropy, most prominent at F4 between 198 and 206 ms (critical  $F$ -value:  $\pm 12.26$ ). Figure 2b displays the grand-average ERPs and the topographic maps for this effect. The other effect, presented in Figure 3a,b, consists of an increase in N1 amplitude (50–140 ms post-onset) for large timing deviants, at fronto-central (AF3, AF4, F3, Fz, F4, FC1, FC2, FC6, F1, F2, FC3 and FC4) and centro-parietal electrodes (C1, Cz, C2, C4, Cz and CPz; critical  $F$ -value:  $\pm 11.22$ ).

Figures 4 and 5 give a more detailed picture of how rhythmic complexity affects the ERPs in the N1 and MMN window. The second factorial analysis performed on deviant minus standard difference waves yielded a main effect of entropy for large deviants in the N1 window (critical  $F$ -value:  $\pm 11.31$ ). More specifically, post hoc comparisons revealed a negative deflection of the difference potential from the zero- to the medium-entropy condition at fronto-central electrodes (FC5 and FC6; time range: 120–150 ms post-onset; critical  $F$ -value:  $\pm 23.42$ ). A further deflection in the same direction was observed from the medium- to high-entropy condition at fronto-central (Fz, F1, FC1 and FC2) and centro-parietal electrodes (Cz, C4, C1 and C2; time range: 60–100 ms post-onset; critical  $F$ -value:  $\pm 25.01$ ). Post hoc comparisons on the small-deviant ERPs revealed that the MMN amplitude was significantly larger in the isochronous than the high-entropy condition (critical  $F$ -value:  $\pm 27.69$ ) between 198 and 222 ms post-onset at fronto-central electrodes (F2, F4, FC2 and FC4), while



**FIGURE 5** Modulation of grand-average ERPs and difference potentials by entropy in the N1 and MMN time windows. Line graph showing the amplitude of standard (STD) and deviant ERPs (DEV), plus deviant minus standard potentials (DW), as a function of stimulus entropy (zero entropy = 0 bit; medium entropy = 1 bit; high entropy = 2 bits). Notice that the N1 and MMN time windows used for this analysis correspond to the 30 ms windows centred at time points with maximal  $F$ -values for large- and small-deviant responses, respectively (see grey shaded area in Figures 2b and 3b)

the differences in MMN amplitude found between isochronous and medium entropy (critical  $F$ -value:  $\pm 27.59$ ;  $F_{\max} = 25.93$  at F6) and between medium and high entropy (critical  $F$ -value:  $\pm 27.59$ ;  $F_{\max} = 15.41$  at C4) did not survive the correction for multiple comparisons.

To further test the hypothesis of a modulation of small-deviant neural response by rhythmic entropy, we performed a linear mixed-effects model analysis on a fixed time window (160–240 ms), known to contain the MMN. We used entropy levels as a fixed-effect variable, individuals as random-effect variable and deviant minus standard MMN amplitude for small deviants as dependent variable. The results show an inverse relationship between entropy in rhythms and MMN amplitude. Specifically, a likelihood ratio test of the full model against a null model revealed a significant decrease in MMN amplitude (Linear mixed effect:  $\chi^2(1) = 15.99$ ,  $p = 0.00006$ ) with increasing entropy.

The corresponding analysis on large-deviant responses did not yield any significant effect.

### 3.3 | Standard- versus deviant-evoked responses

To minimize a potentially confounding contribution of standard responses to the above findings, we conducted a further factorial mass univariate analysis, this time only on ERP standard responses. We used entropy as within-subject factor and the amplitude of the ERPs as dependent variable. This analysis was performed using the same window (50–250 ms) and number of permutations (10,000) as the first one. No main effect of entropy was found (critical  $F$ -value:  $\pm 12.28$ ).

## 4 | DISCUSSION

This work supports the hypothesis that predictive model accuracy and consequently the brain's weighting of neural prediction error are affected by rhythmic complexity. Specifically, we demonstrated that the size of neural prediction error elicited by timing deviations, as reflected in the MMN amplitude, decreases as a function of stimulus entropy. Crucially, we observed this effect only for small, less salient temporal deviants but not for large, more salient deviants. For large deviants, instead, we observed a modulation of N1 in the opposite direction, that is, an increase with increasing stimulus entropy. We interpret these findings in terms of an interaction between effects of temporal regularity and attention on deviant-related responses.

### 4.1 | Timing regularity and pre-attentive deviant-evoked activity

Previous evidence on the effects of timing regularity on (pre-attentive) deviant-evoked responses in auditory tone



streams has been inconsistent. For instance, rhythmic periodicity yielded mixed results on the relevant early sensory ERPs, such as an N1 (deviant) increment (Ford & Hillyard, 1981; Schwartz et al., 2013), an N1 decrement (Harada et al., 2005; Schwartz, Rothermich, Schmidt-Kassow, & Kotz, 2011) or no noticeable effects (e.g. Costa-Faidella et al., 2011; Tavano et al., 2014). The inconsistencies across studies might be due to a number of reasons, including the use of different stimulation paradigms engaging different cognitive processes. For instance, an effect of attention on deviance detection could not be excluded in some studies, given the use of low rate stimuli (<2 Hz; see Heilbron & Chait, 2018). In a recent EEG study, Southwell and Chait (2018) presented listeners with rapid tone sequences—regularly or randomly organized tone streams in two separate runs, containing occasional frequency deviants. Using a fast stimulation rate (>10 Hz) allowed the authors to tap into attention-independent detection processes. They report an effect of timing regularity on early cortical potentials (at 80 ms latency), more specifically a larger N1 response to frequency deviants for regular relative to random stimuli. Their results suggest that deviant detection neural responses are subject to automatic modulation by stimulus regularity (for detailed reviews see Heilbron & Chait, 2018; Khouri & Nelken, 2015). Our results support and extend these findings to the encoding of rhythmic patterns at slower rates (<10 Hz). We observed a greater neural error signal, as reflected by larger MMN amplitudes, for timing violation of isochronous patterns compared to the non-isochronous timing conditions. Unlike in some of the aforementioned studies (Costa-Faidella et al., 2011; Schwartz et al., 2013; Tavano et al., 2014), this result can hardly be explained by an increased positivity of standard-evoked potentials, as no main effect of stimulus entropy was observed on those responses. Overall, these results support the view that deviance detection processes, in addition to neuronal adaptation, provide a major contribution to the magnitude of the neural prediction error (Southwell & Chait, 2018).

## 4.2 | Precision-weighted modulation of neural prediction error by rhythmic complexity

Our study extends the findings reported above to different levels of temporal uncertainty. In previous studies, the effect of temporal regularity on (pre-attentive) deviance detection responses has been investigated by a contrast between isochronous and randomly timed tone streams (Costa-Faidella et al., 2011; Schwartz et al., 2011, 2013; Southwell & Chait, 2018; Tavano et al., 2014). This hints at a qualitative difference between past work and our present approach. While previous work has only been able to address the *sensitivity* of detection-evoked responses to temporal regularity, our work can test the hypothesis of a *dependence*. Limitations

in processing time and memory space constrain the amount of stimulus information (i.e. the distinct interval durations) that can be efficiently extracted and accurately encoded (Drake & Bertrand, 2001; de Fleurian, Blackwell, Ben-Tal, & Müllensiefen, 2017; Snyder, 2000). Following this, we would expect weaker predictive models for more complex rhythmic patterns, and hence a down-weighted neural response to their violations. The decrease in MMN amplitude as a function of entropy observed here for small—but not large—deviants provides clear neurophysiological evidence in support for this hypothesis (see also Imada, Hari, Loveless, McEvoy, & Sams, 1993; Moberget et al., 2008; Takegata & Morotomi, 1999).

Furthermore, the exclusive effect of entropy on small-deviant MMN responses suggests not only a quantitative but also *qualitative* difference in the processing of the two magnitudes of deviations employed here. The two magnitudes were chosen to induce two different types of perceptual deviation in timing: a small deviation with preserved grouping, and a large deviation that would change the grouping, yielding a different “rhythmic contour”. Hereby, we may have tapped into two different aspects of temporal processing: absolute, duration-based timing and relative, grouping-based processing of rhythmic contour. The duration-based timing code entails the encoding of the precise timing of event onsets in a sequence. The grouping-based timing contour would entail a representation of the succession of slow, fast or constant intervals, regardless of their exact size. The rhythmic contour of tonal sequences represents the most recognizable form of music organization (Frasse, 1974; Snyder, 2000). Its violation can be perceived as highly salient and produce involuntary temporal orienting. Changes in the onset timings that preserve the rhythmic contour are typically, although depending on their size, much harder to detect (Dowling, Barbey, & Adams, 1999). This might suggest a privileged status for contour information in the listener's representations. It is possible that representations of high-entropy sequences contain less accurate information about the absolute onset timings but rely on more global grouping characteristics. This could explain the progressive decrease in prediction error (i.e. MMN amplitude) as a function of entropy *only* for small deviants.

Furthermore, our results suggest that the precision-weighting mechanism targeted in this work manifests under conditions of implicit auditory attention, that is, with little or no contamination by top-down processes. Large timing deviations are salient enough to trigger mechanisms of attentional capture. One then would expect a contamination of neural prediction error by attention-related components and, as a result, a masking of the weighting effect. Although supported by recent studies using rapid stimulation paradigms (e.g. Southwell & Chait, 2018), which make difficult the active tracking of individual sounds, this idea requires further investigation.

### 4.3 | The combined effect of temporal regularity and orienting of attention on N1 responses

At first glance, the enhanced N1 observed for large timing deviants in high-entropy rhythms might seem at odds with our discussion above. Specifically, the N1 enhancement seems to contradict the view of a mechanism that down-weights neural responses as the stimulus context becomes harder to model for the brain, and the model more imprecise. In the following, we propose a more comprehensive explanation that takes into account the combined effects of orienting of attention and temporal regularity on the N1 (Lange, 2013).

The modulatory effect of attention on the auditory N1, as an obligatory component of early cortical auditory processing has long been documented (Näätänen & Picton, 1987). Several studies reported an N1 enhancement by large acoustic changes that induce reorienting of attention (e.g. Escera, Alho, Schröger, & Winkler, 2000; Näätänen, 1990; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Schröger, 1996). The enhancement is interpreted as evidence of a redeployment of processing resources towards a salient event. But how might such largely involuntary orienting of attention interact with stimulus regularity in modulating brain cortical activity? In a working model of temporal reorienting, Lange (2013) contrast their effects on N1: orienting of attention leads to an N1 enhancement, stimulus predictability to an attenuation. Isochronous stimuli yield a reduced N1 compared to more complex, non-isochronous rhythms (e.g. Clementz, Barber, & Dzau, 2002; Hsu, Le Bars, Hämäläinen, & Waszak, 2015; Lange, 2009, 2013; Schafer, Amochaev, & Russell, 1981). This can be accounted for by attention-related mechanisms. Listeners' attention is automatically driven towards stimuli perceived as "salient" (Itti, Koch, & Niebur, 1998). In previous studies, an attentional bias of this sort was proposed for randomly timed stimuli (Jones, Alford, Bridges, Tremblay, & Macken, 1999; Macken, Mosdell, & Jones, 1999; Southwell & Chait, 2018; Southwell et al., 2017), which appear to act as potent distractors in visual and auditory tasks (but see Zhao, Al-Aidroos, & Turk-Browne, 2013 for a different account). Irregular timing may indeed lead to an (overall) amplification of sensory and neural responses (Hillyard, Vogel, & Luck, 1998). Hence, we assume here an "additive" effect of attention and irregularity (here, the context entropy) on the auditory N1 (Lange, 2013) when large timing deviations drive the listener's active attention towards the deviant sound (Clementz et al., 2002; Lange, 2009, 2013; Schafer et al., 1981). The decreasing effect of regularity on N1 in turn might counteract the effect of attentional reorienting. This may result in an overall (net) decrease in the auditory N1, as found in our study for isochronous stimuli.

### 4.4 | MMN as a neurophysiological marker of rhythmic complexity

Our neurophysiological results support Shannon entropy as a valuable measure of (perceived) temporal complexity of short rhythmic patterns (Shmulevich & Povel, 2000; Temperley, 2007). Past work attempted to relate rhythmic complexity and neural prediction error by taking a music-theoretical approach: complexity was operationalized as the degree of perceived tension created by going against metrically salient pulses (Bouwer & Honing, 2015; Bouwer, Van Zuijen, & Honing, 2014; Vuust & Witek, 2014). In this respect, music-theoretical analyses have quantified rhythmic complexity in various ways: based on increasing values in the time signature, increasing number of beat subdivisions and estimates of the level of syncopation in notated music (Gómez, Thul, & Toussaint, 2007; Shmulevich & Povel, 2000; Vuust & Witek, 2014). While such measures may relate better to the rhythmic complexity subjectively reported by human subjects than formal mathematical measures (e.g. Shmulevich & Povel, 2000), this may have hindered the use of information-theoretical measures in timing research. This work employed short patterns lacking a metrical time structure. Using such patterns, we showed that the activity of fast (i.e. <200 ms post-onset) and automatic, attention-independent brain mechanisms depends on the amount of information in the sensory input. Our results provide, to the best of our knowledge, the first neurophysiological support on the perceptual validity of information-theoretic measures of rhythmic complexity. They further support the view of the MMN as a pre-attentive, neurophysiological marker of (perceived) stimulus complexity (Boh, Herholz, Lappe, & Pantev, 2011; Lumaca & Baggio, 2016). Future work will extend our current approach to the processing of longer sequences with increasing levels of metricality (e.g. Grube & Griffiths, 2009), taking into account the effects of rhythmic contour and the serial order of time intervals, towards a precisely controlled test of the framework of predictive coding with respect to the metrical beat (Vuust, Dietz, Witek, & Kringelbach, 2018).

### 4.5 | Conclusions

This work reveals a dependence of a neural signature of prediction error, the MMN, to the entropy of temporal patterns. The results obtained are consistent with the idea that MMN amplitude is weighted by the brain's estimated precision of prediction within the given rhythmic context, as quantified here by Shannon entropy. This effect was only observed under pre-attentive and automatic detection of stimulus deviation. This result contributes to the understanding of how the brain automatically acquires an internal model of regularities of an auditory input under different states of temporal

uncertainty. Because of the limited number of interval durations in our experiment, the finding of a relationship between neural prediction error and temporal information content remains somewhat preliminary. Further work, with longer rhythmic stimuli of different levels of complexity and metricity, is necessary to assess the nature of this dependence—linear or non-linear—and to explain it in more details within the framework of predictive coding.

## ACKNOWLEDGEMENTS

The authors thank Giosuè Baggio for useful comments and for providing laboratory resources, and Hella Kastbjerg and Amanda Valbøll for proofreading the manuscript. Center for Music in the Brain is funded by the Danish National Foundation (DNRF117).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA ACCESSIBILITY

Data and materials of this study are archived online at <https://osf.io/x98mb/>

## AUTHOR CONTRIBUTIONS

ML and NTH designed the research. ML performed the research. ML and NTH analysed the data. NTH made the figures. ML wrote the article, with contributions by MG and NTH. PV and EB supervised the work and contributed to the manuscript.

## ORCID

Massimo Lumaca  <https://orcid.org/0000-0002-3432-3911>

## REFERENCES

- Arnal, L. H., & Giraud, A. L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*, 390–398. <https://doi.org/10.1016/j.tics.2012.05.003>
- Bates, D., Maechler, M., & Bolker, B. (2012). *lme4: Linear mixed-effects models using S4 classes*.
- Bendixen, A., SanMiguel, I., & Schröger, E. (2012). Early electrophysiological indicators for predictive processing in audition: A review. *International Journal of Psychophysiology*, *83*, 120–131.
- Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology*, *30*, 518–524.
- Boh, B., Herholz, S. C., Lappe, C., & Pantev, C. (2011). Processing of complex auditory patterns in musicians and nonmusicians. *PLoS One*, *6*, e21458.
- Bouwer, F. L., & Honing, H. (2015). Temporal attending and prediction influence the perception of metrical rhythm: Evidence from reaction times and ERPs. *Frontiers in Psychology*, *6*, 1094.
- Bouwer, F. L., Van Zuijlen, T. L., & Honing, H. (2014). Beat processing is pre-attentive for metrically simple rhythms with clear accents: An ERP Study. *PLoS One*, *9*, e97467.
- Clementz, B. A., Barber, S. K., & Dzau, J. R. (2002). Knowledge of stimulus repetition affects the magnitude and spatial distribution of low-frequency event-related brain potentials. *Audiology and Neurotology*, *7*, 303–314.
- Cohen, J. E. (1962). Information theory and music. *Systems Research and Behavioral Science*, *7*, 137–163.
- Costa-Faidella, J., Baldeweg, T., Grimm, S., & Escera, C. (2011). Interactions between “What” and “When” in the auditory system: Temporal predictability enhances repetition suppression. *Journal of Neuroscience*, *31*, 18590–18597.
- 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*, 9–21.
- Dowling, W. J., Barbey, A., & Adams, L. (1999). Melodic and rhythmic contour in perception and memory. In S. W. Yi (Ed.), *Music, mind, and science*, (pp. 166–188). Seoul: Seoul National University Press.
- Drake, C., & Bertrand, D. (2001). The quest for universals in temporal processing in music. *Annals of the New York Academy of Sciences*, *930*, 17–27.
- Elliott, M. T., Wing, A. M., & Welchman, A. E. (2014). Moving in time: Bayesian causal inference explains movement coordination to auditory beats. *Proceedings of the Royal Society B*, *281*, 20140751.
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neurotology*, *5*, 151–166.
- Ewbank, M. P., Lawson, R. P., Henson, R. N., Rowe, J. B., Passamonti, L., & Calder, A. J. (2011). Changes in “Top-Down” connectivity underlie repetition suppression in the ventral visual pathway. *Journal of Neuroscience*, *31*, 5635–5642.
- Feldman, H., & Friston, K. J. (2010). Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience*, *4*, 215.
- Fields, E. C. (2017). *Factorial Mass Univariate ERP Toolbox* [Computer software]. Retrieved from <https://github.com/ericfields/FMUT/releases>
- de Fleurian, R., Blackwell, T., Ben-Tal, O., & Müllensiefen, D. (2017). Information-theoretic measures predict the human judgment of rhythm complexity. *Cognitive Science*, *41*, 800–813.
- Ford, J. M., & Hillyard, S. A. (1981). Event-related potentials (ERPs) to interruptions of a steady rhythm. *Psychophysiology*, *18*, 322–330.
- Fraisse, P. (1974). *Psychologie du rythme*. Paris: Presses Universitaires de France.
- Friston, K. (2002). Beyond phrenology: What can neuroimaging tell us about distributed circuitry? *Annual Review of Neuroscience*, *25*, 221–250.
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *360*, 815–836.
- Gómez, F., Thul, E., & Toussaint, G. T. (2007). An experimental comparison of formal measures of rhythmic syncopation. In *Proceedings of the International Computer Music Conference (Copenhagen)* (pp. 101–104).

- Groppe, D. M., Urbach, T. P., & Kutas, M. (2011a). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. *Psychophysiology*, *48*, 1711–1725.
- Groppe, D. M., Urbach, T. P., & Kutas, M. (2011b). Mass univariate analysis of event-related brain potentials/fields II: Simulation studies. *Psychophysiology*, *48*, 1726–1737.
- Grube, M., & Griffiths, T. D. (2009). Metricity-enhanced temporal encoding and the subjective perception of rhythmic sequences. *Cortex*, *45*, 72–79.
- Harada, N., Masuda, T., Endo, H., Nakamura, Y., Takeda, T., & Tonoike, M. (2005). The effect of 1/f fluctuation in inter-stimulus intervals on auditory evoked mismatch field. *Neuroscience Letters*, *379*, 223–228.
- Heilbron, M., & Chait, M. (2018). Great expectations: Is there evidence for predictive coding in auditory cortex? *Neuroscience*, *389*, 54–73.
- Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society B*, *353*, 1257–1270.
- Hsu, Y. F., Le Bars, S., Hämäläinen, J. A., & Waszak, F. (2015). Distinctive representation of mispredicted and unpredicted prediction errors in human electroencephalography. *Journal of Neuroscience*, *35*, 14653–14660.
- Imada, T., Hari, R., Loveless, N., McEvoy, L., & Sams, M. (1993). Determinants of the auditory mismatch response. *Electroencephalography and Clinical Neurophysiology*, *87*, 144–153.
- Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *20*, 1254–1259.
- Jones, D., Alford, D., Bridges, A., Tremblay, S., & Macken, B. (1999). Organizational factors in selective attention: The interplay of acoustic distinctiveness and auditory streaming in the irrelevant sound effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 464–473.
- Khouri, L., & Nelken, I. (2015). Detecting the unexpected. *Current Opinion in Neurobiology*, *35*, 142–147.
- Knolle, F., Schröger, E., Baess, P., & Kotz, S. A. (2012). The cerebellum generates motor-to-auditory predictions: ERP lesion evidence. *Journal of Cognitive Neuroscience*, *24*, 698–706.
- Lange, K. (2009). Brain correlates of early auditory processing are attenuated by expectations for time and pitch. *Brain and Cognition*, *69*, 127–137.
- Lange, K. (2013). The ups and downs of temporal orienting: A review of auditory temporal orienting studies and a model associating the heterogeneous findings on the auditory N1 with opposite effects of attention and prediction. *Frontiers in Human Neuroscience*, *7*, 263.
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213.
- Luck, S. J. (2014). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.
- Lumaca, M., & Baggio, G. (2016). Brain potentials predict learning, transmission and modification of an artificial symbolic system. *Social Cognitive and Affective Neuroscience*, *11*, 1970–1979.
- Lumaca, M., Haumann, N. T., Vuust, P., Brattico, E., & Baggio, G. (2018). From random to regular: Neural constraints on the emergence of isochronous rhythm during cultural transmission. *Social Cognitive and Affective Neuroscience*, *13*, 877–888.
- Macken, W. J., Mosdell, N., & Jones, D. M. (1999). Explaining the irrelevant-sound effect: Temporal distinctiveness or changing state? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 810–814.
- May, P., Tiitinen, H., Ilmoniemi, R. J., Nyman, G., Taylor, J. G., & Näätänen, R. (1999). Frequency change detection in human auditory cortex. *Journal of Computational Neuroscience*, *6*, 99–120.
- Moberget, T., Karns, C. M., Deouell, L. Y., Lindgren, M., Knight, R. T., & Ivry, R. B. (2008). Detecting violations of sensory expectancies following cerebellar degeneration: A mismatch negativity study. *Neuropsychology*, *46*, 2569–2579.
- Monahan, C. B. (1985). *Parallels between pitch and time: The determinants of musical space*. Unpublished doctoral dissertation, University of California, Los Angeles, CA.
- Näätänen, R. (1990). The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behavioral and Brain Sciences*, *13*, 201–233.
- Näätänen, R., Gaillard, A. W. K., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica*, *42*, 313–329.
- Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*, 2544–2590.
- Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: A review and an analysis of the component structure. *Psychophysiology*, *24*, 375–425.
- Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D. Y., & Schröger, E. (2002). Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *NeuroImage*, *15*, 167–174.
- Paavilainen, P. (2013). The mismatch-negativity (MMN) component of the auditory event-related potential to violations of abstract regularities: A review. *International Journal of Psychophysiology*, *88*, 109–123.
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rao, R. P. N. (2005). Bayesian inference and attentional modulation in the visual cortex. *NeuroReport*, *16*, 1843–1848.
- Ravignani, A., & Madison, G. (2017). The paradox of isochrony in the evolution of human rhythm. *Frontiers in Psychology*, *8*, 1820.
- Schafer, E. W. P., Amochaev, A., & Russell, M. J. (1981). Knowledge of stimulus timing attenuates human evoked cortical potentials. *Electroencephalography and Clinical Neurophysiology*, *52*, 9–17.
- Schröger, E. (1996). A neural mechanism for involuntary attention shifts to changes in auditory stimulation. *Journal of Cognitive Neuroscience*, *8*, 527–539.
- Schwartz, M., Farrugia, N., & Kotz, S. A. (2013). Dissociation of formal and temporal predictability in early auditory evoked potentials. *Neuropsychology*, *51*, 320–325.
- Schwartz, M., Rothermich, K., Schmidt-Kassow, M., & Kotz, S. A. (2011). Temporal regularity effects on pre-attentive and attentive processing of deviance. *Biological Psychology*, *87*, 146–151.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, *27*, 379–423.
- Shmulevich, I., & Povel, D. J. (2000). Measures of temporal pattern complexity. *Journal of New Music Research*, *29*, 61–69.

- Snyder, B. (2000). *Music and memory: An introduction*. Cambridge, MA: MIT Press.
- 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*, 372, 20160105.
- Southwell, R., & Chait, M. (2018). Enhanced deviant responses in patterned relative to random sound sequences. *Cerebral Cortex*, 109, 92–103.
- Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, 11, 1004–1006.
- Takegata, R., & Morotomi, T. (1999). Integrated neural representation of sound and temporal features in human auditory sensory memory: An event-related potential study. *Neuroscience Letters*, 274, 207–210.
- Tavano, A., Widmann, A., Bendixen, A., Trujillo-Barreto, N., & Schröger, E. (2014). Temporal regularity facilitates higher-order sensory predictions in fast auditory sequences. *European Journal of Neuroscience*, 39, 308–318.
- Temperley, D. (2007). *Music and probability*. Cambridge, MA: The MIT Press.
- Toussaint, G. T. (2013). *The geometry of musical rhythm: What makes a "Good" rhythm good?* Boca Raton, FL: CRC Press.
- Vuust, P., Dietz, M. J., Witek, M., & Kringelbach, M. L. (2018). Now you hear it: A predictive coding model for understanding rhythmic incongruity. *Annals of the New York Academy of Sciences*, 1423, 19–29.
- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music - Brain responses to rhythmic incongruity. *Cortex*, 45, 80–92.
- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, 5, 1111.
- Wacongne, C., Changeux, J. P., & Dehaene, S. (2012). A neuronal model of predictive coding accounting for the mismatch negativity. *Journal of Neuroscience*, 32, 3665–3678.
- Winkler, I., Denham, S. L., & Nelken, I. (2009). Modeling the auditory scene: Predictive regularity representations and perceptual objects. *Trends in Cognitive Sciences*, 13, 532–540.
- Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, 24, 667–677.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Lumaca M, Trusbak Haumann N, Brattico E, Grube M, Vuust P. Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *Eur J Neurosci*. 2019;00:1–13. <https://doi.org/10.1111/ejn.14329>