

Electrophysiological evidence of temporal preparation driven by rhythms in  
audition

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## **Abstract**

Reaction speed to respond to an auditory target stimulus is enhanced when it is presented at a moment matching the temporal structure of a preceding regular rhythm (Sanabria, Capizzi, & Correa, 2011). However, the electrophysiological correlates of this behavioural enhancement remain unknown. In the present study, participants performed a simple auditory reaction time task in which a regular rhythm with either a fast (400 ms interval between the tones making the rhythm) or a slow (900 ms interval between the tones making the rhythm) was presented prior to the target. The target tone could be presented, with the same probability, 400 ms or 900 ms after the offset of the rhythmic sequence. The behavioural results showed that the fastest responses were obtained when the target appeared in synchrony with the preceding rhythm (e.g., the target was presented 900 ms after the slow rhythm). This behavioural benefit was accompanied by amplitude modulations of the N1 potential and the P2 potential, both related to the processing of the auditory target. Crucially, these electrophysiological modulations were obtained in both the fast and slow rhythm conditions. The current research demonstrates that rhythms with different paces can drive temporal preparation exogenously, affecting early and late stages of auditory neural processing.

**Keywords:** predictive coding, timing, temporal expectation, exogenous temporal orienting, Repetition suppression, Attentional Entrainment, event-related potentials, N1, P2, MMN.

Temporal regularities of the environment have probably promoted the evolution of cognitive skills such as temporal preparation. Temporal preparation can be defined as the ability to enhance cognitive processing in anticipation of the moment of occurrence of a relevant stimulus, optimizing the processing of that stimulus when it actually occurs (see Nobre, Correa, & Coull, 2007, for a review). Empirical evidence shows that temporal preparation can be triggered by regular rhythms, that is, the isochronous presentation of a stimulus sequence. For example, a stimulus onset matching the timing of an auditory regular rhythm is discriminated better than a stimulus preceded by an irregular rhythm (Barnes & Jones, 2000; Jones, Moynihan, MacKenzie, & Puente, 2002). Recent studies have further shown that the effect of temporal preparation guided by rhythms generalizes to the visual modality and other behavioural measures such as RT (Correa & Nobre, 2008; Doherty, Rao, Mesulam, & Nobre, 2005) and that the effect is not constrained to a single rhythmic pace and temporal interval (Sanabria, Capizzi, & Correa, 2011).

In Sanabria et al.'s (2011; Experiment 3) study we presented regular rhythms at two different paces manipulated on a trial-by-trial basis. The fast rhythm consisted of the presentation of a sequence of six tones separated by intervals of 400 ms, whereas the slow rhythm included a 900-ms interval between tones (see Figure 1). Each rhythm pace was associated to different foreperiods (200, 400, 900, 1400, and 1600 ms) with equal probability ( $p = 0.2$ ). The results showed that RTs to respond to the auditory target stimulus presented after the rhythm were faster for targets appearing at short foreperiods (200 and 400) when the preceding rhythm was fast rather than slow. On the other hand, RTs were faster for targets appearing at the long foreperiods (900 and 1400) when the preceding rhythm was slow rather than fast. This latter finding was crucial to rule out that our effects were just due to higher arousing properties of fast vs. slow rhythms. This

study suggests that auditory RT performance is fastest for targets appearing at the foreperiod matching the pace of a regular rhythm.

The above behavioural studies have consistently supported that regular rhythms can enhance both speed and accuracy of task performance. Sanabria et al. (Sanabria, Capizzi, & Correa, 2011) went a step further by showing that temporal preparation guided by rhythms depended on the particular temporal matching between the rhythmic pace and the moment of target appearance, and not simply on the temporal regularity of the rhythm. However, the neural correlates of such RT behavioural improvement remain unknown. The aim of the present research was to study the electrophysiological correlates of temporal preparation guided by two rhythms of different paces, specifically in the auditory modality.

When compared to irregular rhythms, regular rhythms seem to facilitate later stages of cognitive processing as indexed by an enhancement of the P3 event-related potential (ERP) linked to the target onset (Lange, 2009, 2010; Schmidt-Kassow, Schubotz, & Kotz, 2009; Schwartz, Rothermich, Schmidt-Kassow, & Kotz, 2011). Regarding early auditory processing, one could expect regular rhythms to enhance the N1 potential, an ERP peaking around 100 ms after an auditory stimulus with a central distribution over the scalp, generated in the primary and secondary auditory cortices (Näätänen & Picton, 1987). In effect, the amplitude of the auditory N1 is increased for expected vs. unexpected target onsets in temporal-orienting studies, where symbolic temporal cues are used to indicate the most probable moment of target appearance (Lampar & Lange, 2011). However, the scarce evidence regarding the effect of temporal preparation induced by rhythms on the auditory N1 reveals a different pattern of results.

Lange (2009) investigated the effect of rhythms on the auditory N1 potential by asking participants to detect a 10-ms silent gap that was present in a small proportion of the auditory targets. The target could be preceded by either a regular or irregular rhythm, which consisted of a sequence of 12 tones inter-separated by an interval that was fixed (550 ms) or variable (random durations between 300 and 800 ms), respectively. The rhythm was followed by a constant foreperiod of 1650 ms (matching three steps of the 550-ms rhythm), and then the target appeared. The results of two experiments consistently showed that the regular rhythm attenuated the N1 amplitude as compared to the irregular rhythm. Lange's results were consistent with the findings of an earlier study by Schafer et al. (1981; see also Costa-Faidella, Baldeweg, Grimm and Escera, 2011). These authors reported an attenuated amplitude and earlier latency of the auditory N1, P2, N2 and P3 potentials when the target tone was presented after a regular sequence of visual events, compared to a condition in which the visual events formed a temporally irregular sequence.

In a subsequent experiment, Lange (2010) further tested whether the N1 attenuation effect was driven by temporal preparation. In contrast to her previous experiment (and to Schafer et al.'s 1981, study) where the foreperiod was constant and therefore predictable, the foreperiod duration was variable such that the target could appear after either 800, 1100 or 1400 ms. The N1 attenuation was mainly expected in the 1100-ms condition, as this was the only foreperiod matching (two steps of) the 550-ms regular rhythm. However, in contrast to her previous study, the results showed that the amplitude of the N1 elicited by the target was increased following regular as compared to irregular sequence of tones (this effect was restricted to the left hemisphere). Moreover, the

foreperiod manipulation (different durations with a similar a priori probability that changed trial-by-trial) led to decreased RTs and enhanced N1 amplitudes on left electrodes with increasing foreperiod durations (i.e., the foreperiod effect; see Niemi & Näätänen, 1981, for a review). Hence, it might be possible that any attenuation of the N1 potential by regular rhythms was not observed in this experiment because it was masked by the enhancement produced by the foreperiod effect. In fact, interactions between the effects of regular rhythms and foreperiod duration have been reported in the visual modality (Correa & Nobre, 2008; Rohenkohl, Coull, & Nobre, 2011).

Two main issues motivated the present research. First, to the best of our knowledge, there are not ERP studies investigating the effect of regular rhythms with different paces on auditory target processing, since previous studies have always compared the effect of an isochronous regular with the effect of an irregular rhythm. In the present study, the auditory target was presented after a time interval that could match or mismatch the rhythmic pace of the preceding regular rhythm. That way, we were able to investigate whether the effect of a regular rhythm on auditory target ERPs in a simple RT task depended on the temporal matching between the particular rhythmic pace and the elapsed time prior to the onset of the target, or simply on the temporal regularity of the rhythm. Second, the scarce extant ERP evidence does not make clear the nature of the effect of regular rhythms on auditory processing.

In order to achieve our purpose, we designed an experiment with the following main manipulations. As in our previous research (Sanabria et al., 2011), temporal preparation was induced by a regular rhythm of either a fast or a slow pace. In the current simpler design, only two foreperiods were used so that the target tone could appear at either a

short (400 ms) or long (900 ms) foreperiod. Since rhythm paces and foreperiods were paired at 50%, temporal expectations would emerge automatically from the rhythm itself rather than from cuing probability (Jones et al., 2002). That is, a fast rhythm would induce participants to expect the target early (after a foreperiod of 400 ms), whereas a slow rhythm would induce participants to expect a late target onset (after 900 ms). Therefore, the pure effect of the rhythm, without the influence of probabilities involved in temporal orienting and foreperiod effects, could be measured at the short foreperiod. Catch trials (16.7%) were included to prevent the robust foreperiod effect that could be masking our effect of interest at the long interval (see Sanabria et al., Experiment 2), in order to measure the rhythm effect also at the long foreperiod.

The abovementioned manipulations allowed us to compare directly the pure effects of temporal preparation based on two regular rhythms just differing in pace, in contrast to previous studies that have compared regular with irregular rhythms (e.g., Lange, 2009), while controlling for other sources of temporal preparation based on temporal orienting and foreperiod effects. If the mechanism underlying temporal preparation guided by rhythms is analogous to temporal orienting, we should find that regular rhythms enhance the auditory N1 (Lange & Röder, 2006; Sanders & Astheimer, 2008). However, the results by Lange (2009) and Schafer et al. (1981; see also Costa-Faidella et al., 2011) led us to expect a different pattern of results, with an attenuation of the N1 and P2 potentials when the target tone would appear at the moment matching the preceding rhythm.

Importantly, we expected to obtain an influence of both the fast and slow rhythmic paces on auditory target ERPs, indicating that the rhythm effect on auditory processing depended on the particular matching between the rhythm pace and the moment of target appearance.

## **Methods**

*Participants.* Sixteen undergraduates (seven females, 2 left-handed, age range: 18-26 years old, mean age: 22 years old) from the University of Granada participated in the study and were compensated with 20 euro. All participants reported normal or corrected to normal vision, had no history of neurological disorders, and gave informed consent prior to the start of the experiment. Data from four participants were discarded from the analyses due to excessive artefacts in the EEG recording. The experiment was conducted in accordance with the ethical guidelines of the local committee.

*Apparatus and stimuli.* Two computers were used to conduct the experiment. An Intel Core 2 Duo PC computer connected to a 17" LCD monitor with E-prime software (Schneider, Eschman, & Zuccolotto, 2002) was used for stimulus presentation and to collect participants' responses. A Power PC G5 Apple (Mac Os 10.4.10) with a high-density 128-electrode EEG system (*Electrical Geodesics, Inc.*) was used for EEG recording. The auditory stimuli were presented through two loudspeakers, one located at each side of the monitor. The viewing distance was approximately 60 cm. The auditory rhythm consisted of a sequential presentation of six 50-ms pure tones separated by either 400 ms (fast rhythmic pace) or 900 ms (slow rhythmic pace). The first five tones (5 ms rise and fall times) had a frequency of 700 Hz. The last tone in the sequence (the warning signal) had a frequency of 1000 Hz. The target sound was a 50-ms pure tone with a frequency of 400 Hz. All sounds were presented at a clearly audible and comfortable intensity ( $\approx 70$  dB). The fixation point consisted of a grey plus sign subtending  $1.5^\circ \times 1.5^\circ$ , and presented on the centre of a black background. This fixation point remained on and steady during the trial and went off after the participant's response.

*Procedure.* Participants sat on a chair in front of the computer in a silent and dimly illuminated room. They were given verbal and written instructions to respond to the appearance of the target tone as fast as possible, while avoiding anticipations, by pressing the space bar with their dominant index finger. Participants were told that the last tone in the rhythm sequence marked the beginning of the preparatory interval. At the beginning of the experimental session participants listened to the target tone to ensure that they would discriminate it from the rhythm tones. A trial started with the presentation of the fixation point, which remained on the screen until the end of the trial. After an interval with a random duration between 1000 and 1500 ms on every trial, either the fast or slow auditory rhythmic pace was presented. The sixth tone in the auditory sequence marked the end of the rhythmic sequence and the beginning of the foreperiod. The target appeared after a foreperiod of either 400 or 900 ms, which varied randomly across trials. A maximum of 2000 ms was allowed to respond. The inter-trial-interval was set to 1000 ms (see Figure 1). Visual feedback was provided on both omissions and anticipatory errors, i.e., when participants responded prior to the presentation of the target.

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INSERT FIGURE 1

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*Design.* The experiment constituted a within-subjects design with the independent variables of Rhythmic pace (fast pace– 400 ms or slow pace– 900 ms) and Foreperiod (400, 900 ms). Each rhythm pace was associated to both short and long foreperiods (400 and 900 ms) with equal probability ( $p = 0.50$ ), i.e., the pace of the rhythm did not predict the onset time of the target. Participants completed a practice block of 10 trials and 14 experimental blocks of 24 trials each. The target was absent on four trials on each block (i.e., 16.7% of the trials). Therefore, five trials were presented for each combination of

the rhythm and foreperiod conditions. Data from the practice block and catch trials were not included in the analyses. Participants were allowed to rest after each block of trials.

### *Electrophysiological recording and analysis*

Electrophysiological activity was recorded from 128 surface electrodes [*Electrical Geodesics, Inc. (EGI)*], referenced to the vertex channel. The electrodes located above and beneath the eyes, and to the left and right of the external canthi of the eyes were used to detect blinks and eye movements. The EEG net was connected to an AC-coupled, high-input impedance amplifier (200 M $\Omega$ ); impedances were kept below 50k $\Omega$ , as recommended for the Electrical Geodesics high-input impedance amplifiers. The signal was amplified, filtered (0.1 to 100-Hz band pass) and digitized at a sampling rate of 250 Hz (16 bits A/D converter).

Data were filtered off-line with a 1-30 Hz bandpass filter. The continuous EEG recording was segmented into epochs, 200 ms before and 600 ms after target onset. These epochs were then submitted to processing for identification of artefacts. Epochs showing an excessively noisy EEG ( $\pm 100 \mu\text{V}$  on 10 channels), eye-movements artefacts (blinks or saccades:  $\pm 50 \mu\text{V}$  on EOG channels) were rejected. Data from individual channels that were consistently bad (when more than 20% of the trials were bad) for a specific subject were replaced using a spherical interpolation algorithm [mean of 1.8 ( $\pm 3.8$  s.e.) channels per subject; Perrin, Pernier, Bertrand, & Echallier, 1989)]. Data from trials with incorrect behavioural responses, reaction times (RTs) above or below 2 standard deviations from the mean, anticipations (i.e., responses before target onset, 0.69 %) and responses to catch trials (1.2 %) were also excluded from the EEG and RT analyses. This data trimming resulted in a rejection of the 15% of the trials for the EEG analyses and 4% for the RT analysis.

Four group-averaged ERP waveforms were constructed according to Rhythmic pace (slow, fast) and Foreperiod (400, 900) experimental conditions to investigate the effect of the rhythmic pace and foreperiod on responses to the target tone. ERPs were re-referenced to the average to eliminate the effects of reference-site activity (Tucker, Liotti, Potts, Russell, & Posner, 1994). The 50-ms pre-stimulus epoch and 50-ms post-stimulus epoch served as baseline. The 50-ms post-stimulus epoch was applied to avoid overlapping effects from the preceding CNV wave (cf. Correa & Nobre, 2008; Correa, Lupiáñez, Madrid, & Tudela, 2006; Griffin, Miniussi, & Nobre, 2002; Lampar & Lange, 2011; see also Woldorff, 1993). Voltage and latency analyses were focused on a temporal window (128ms to 168ms) that included the peak of the N1 evoked by the target tone. Average voltage and latency values of 12 central electrodes (31, 7, 107, 106, 38, 32, VREF, 81, 88, 55, 54, 80; see Figure 2; cf. Lange 2009; 2010) were included in the analyses.

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INSERT FIGURE 2  
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## *Results*

### *Behavioural results*

Participants' mean RTs in response to the target tone were submitted to a repeated measures analysis of variance (ANOVA) with the factors of Rhythm (fast, slow) and Foreperiod (400, 900). The analysis revealed a significant main effect of Foreperiod,  $F(1,11)=12.61, p<.01$ , partial  $\eta^2=.53$ , with participants responding more rapidly after the 400 ms (286 ms) than after the 900 ms (309 ms) foreperiod. Crucially, the interaction between Rhythm and Foreperiod was significant,  $F(1,11)= 17.97, p< .01$ , partial  $\eta^2=.62$  (see Figure 3). Further hypothesis-driven comparisons revealed that, at the 900-ms

foreperiod, participants were faster after the slow rhythm than the fast rhythm (299 ms and 319 ms, respectively),  $F(1,11)=6.10, p=.03$ . The difference between the fast and slow rhythm (282 ms and 289 ms, respectively) at the 400 ms foreperiod failed to reach statistical significance,  $F(1,11)=1.13, p=.3$ . Regarding the typical foreperiod effect (i.e., faster RT at the longer foreperiod than at the shorter foreperiod), it was significantly reversed in the fast rhythm condition (282 ms and 319 ms for the short and long foreperiod, respectively),  $F(1,11)=30.31, p<.001$ , while it failed to reach significance in the slow rhythm condition (289 ms and 299 ms for the short and long foreperiod, respectively),  $F(1,11)=1.61, p=.23$ .

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INSERT FIGURE 3

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#### *ERP results*

A repeated measures ANOVA with the factors of Rhythm (fast, slow) and Foreperiod (400, 900) was performed on mean amplitude voltages within a time window from 128ms to 168ms that included the negative voltage peak.

The ANOVA on the amplitude data revealed a significant interaction between Rhythm and Foreperiod,  $F(1,11)=9.83, p<.01$ , partial  $\eta^2=.47$ . Specifically, at the short foreperiod, the difference between the two rhythm conditions was significant,  $t(11)=3.0, p=.01$ , with an attenuation of the N1 potential following the fast rhythm ( $-0.91 \mu\text{V}$ ) with respect to the slow rhythm ( $-1.56 \mu\text{V}$ ). The difference between the two rhythm conditions at the long foreperiod also reached statistical significance,  $t(1,11)=2.21, p=.049$  (see Figure 4). This time, the N1 potential was attenuated following the slow rhythm ( $-1.00$

$\mu\text{V}$ ) as compared to the fast rhythm ( $-1.60 \mu\text{V}$ ). None of the other two terms in the ANOVA reached statistical significance (both  $F_s < 1$ ).

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INSERT FIGURE 4  
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A similar ANOVA within a time window from 215ms to 255ms that included the P2 peak was conducted on the voltage data. The ANOVA on the voltage data revealed a significant interaction between Rhythm and Foreperiod,  $F(1,11)=27.68, p < .001, \eta^2=.71$ . Further comparisons showed a larger P2 for the fast rhythm ( $2.63 \mu\text{V}$ ) than for the slow rhythm ( $1.46 \mu\text{V}$ ) at the 400-ms foreperiod,  $t(11)=2.71, p=.01$ , and a larger P2 for the slow rhythm ( $2.61 \mu\text{V}$ ) than for the fast rhythm ( $1.51 \mu\text{V}$ ) at the 900-ms foreperiod,  $t(11)=2.89, p < .01$ . Neither the main effect of Rhythm nor the main of Foreperiod were significant (both  $F_s < 1$ ).

## **Discussion**

The main aim of the current research was to investigate the effect of temporal preparation guided by regular rhythms of different paces on auditory processing. Together with the fact that there was not any prior ERP research comparing the effects of two regular rhythms with different paces, the few studies using regular vs. irregular rhythms had reported inconclusive findings regarding whether the amplitude of the auditory N1 and P2 potentials are either attenuated, enhanced, or unaffected by the rhythms (Lange, 2009, 2010; see also Schafer et al., 1981). In the current study, we measured pure effects of

regular rhythms by controlling for temporal orienting effects by means of pairing rhythm paces (fast, slow) with foreperiods (short, long) at 50%. Thus, the pure effect of rhythm, without the influence of any a priori probability, was measured at both foreperiods.

Additionally, the inclusion of a high proportion of catch trials resulted in a modulation of the foreperiod effect, which allowed us to measure rhythm effects also at the long foreperiod, replicating our previous study (Sanabria et al., 2011). Our results showed that temporal preparation guided by rhythms speeded up RTs to auditory stimuli and influenced early and late stages of auditory processing.

The behavioural data showed that the typical foreperiod effect was reversed significantly in the fast rhythm condition of this experiment, which confirmed that the foreperiod effect was controlled effectively. The modulation of the typical foreperiod effect allowed us to observe significant effects of rhythm at the long foreperiod, replicating our previous behavioural study (Sanabria et al., 2011). In that study, we also found that the rhythm RT effect was not significant at the short foreperiod exactly matching the rhythm, but it was mainly obtained at the shortest foreperiod (200 ms), suggesting that temporal preparation induced by a 400-ms rhythmic pace was anticipated to an earlier time point (for similar evidence, see Correa, Kane, Lupiáñez, & Nobre, 2007; Griffin, Miniussi, & Nobre, 2001; Rohenkohl & Nobre, 2011; Sanabria et al., 2011). It may also be possible that, in the present study (and in Sanabria et al.'s, 2011, study), we measured a RT floor effect in the 400-ms foreperiod, masking any significant effect of the fast rhythm at that foreperiod.

The analysis of the N1 mean amplitude elicited by the auditory target revealed an interaction between rhythm pace and foreperiod duration, such that the N1 was attenuated when the target appeared at the foreperiod matching the preceding rhythm with respect to

the temporal mismatching conditions. A significant effect of the rhythm was obtained at both foreperiods: at the short foreperiod, the fast rhythm attenuated the auditory N1 in relation to the slow rhythm, whereas at the long foreperiod the slow rhythm attenuated the N1 in relation to the fast rhythm.

The N1 amplitude effect shown in the two rhythm conditions and at both foreperiods represent a novel finding since, to date, researchers had only compared regular with irregular sequences of tones (e.g., Lange, 2009). Therefore, our results demonstrate that the influence of temporal preparation driven by rhythms on auditory processing depends on the particular rhythm pace and the particular moment of target appearance and not simply on the temporal regularity of the auditory rhythm sequence. This result goes beyond previous accounts (e.g., Costa-Faidella et al., 2011; Lange, 2009), and supports once again the flexibility of temporal preparation driven by rhythms (i.e., it was not restricted to a single rhythm or foreperiod; see Sanabria et al., 2011).

Our result regarding the N1 potential was in line with a previous report by Lange (2009; see also Costa-Faidella et al., 2011; Schafer et al., 1981). Although several methodological differences between Lange's and the present study preclude clear comparisons, both procedures have in common the absence of distributions of intervals typically leading to the probability of target appearance increasing with time. The absence of the typical foreperiod effect might then be a relevant condition to observe the N1 attenuation by regular rhythms.

In the short foreperiod condition of the present experiment, one could have explained the attenuated N1 following the fast rhythm as reflecting neural refractoriness, i.e., a decrease

response of the auditory ERP generators for a critical period of time after the presentation of the last auditory stimulus in the rhythm sequence (see Budd, Barry, Gordon, Rennie, and Michie, 1998; Näätänen and Picton, 1987, for discussion on this issue). However, if the effect at the short foreperiod was due to auditory refractoriness one should have expected no effect of the rhythm at the long foreperiod. In fact, the experimental condition less prone to neural refractoriness was that of the long foreperiod following a slow rhythm having the longest time interval between the offset of the rhythm and the target tone. However, the N1 potential was still attenuated in that condition with respect to the fast rhythm condition. Therefore, the effect at the 900 ms seems to rule out any explanation of our effects in terms of neural refractoriness.

In our study, the fast and slow rhythm differed in their temporal structure, which might have affected the representation of the temporal regularity (e.g., Winkler, Schröger, Cowan, 2001). This change in the regularity representation could have resulted in different effects of each rhythm on the processing of the frequency deviance present between the last tone in the rhythm and the target tone. However, finding the behavioural (and electrophysiological) effect at the 900 ms foreperiod suggests that participants were grouping the auditory stimuli in the slow rhythm condition as part of the same auditory sequence (cf. Bregman, 1990) in a similar way as in the fast rhythm condition. Moreover, the behavioural improvements reported for the slow rhythm supports the flexible nature of the mechanism for temporal preparation based on rhythms (i.e., the effect was not the result of a rigid alerting process; see also Correa & Nobre, 2008), and complements previous research mainly showing facilitation effects when comparing an irregular rhythm to a single fixed regular rhythm (e.g., Doherty et al., 2005; Jones et al., 2002).

Given that the current design involves a comparison between conditions where rhythm and foreperiod were matching vs. mismatching, one interpretation of the N1 result could consider our effect as reflecting a mismatch negativity (MMN) in the time domain (for a recent review, see Bendixen, Sanmiguel, & Schröger, 2011). In effect, it has been shown that the omission of an auditory stimulus in a regular temporal sequence produces an ERP negativity (i.e., MMN) that is similar to that found in the present experiment (e.g., Takegata, Paavilainen, Näätänen and Winkler, 2001).

Interestingly, some authors have interpreted the MMN as a hallmark of predictive coding, a hypothesis that assumes that the brain is able to extract regularities in the environment to predict the incoming events (see Wacongne, Changeux, and Dehaene, 2012; Bendixen et al., 2011; for reviews). If the prediction differs from the actual stimulus, then the MMN occurs. Therefore, the effect on the N1 potential reported in this paper can be interpreted either as attenuation by the temporal preparation in matching conditions or as enhancement of the N1 potential in temporal mismatching conditions (resulting in a temporal MMN). A neutral condition could have helped to differentiate between these two alternatives. However, finding a “true” neutral condition is not straightforward and may complicate rather than clarify the interpretation of the data pattern (see Jonides & Mack, 1984, for a discussion on this matter). In any case, the interpretation of N1 attenuation by the temporal preparation driven by rhythmic pace is in line with previous accounts that have compared regular with irregular rhythms (Lange 2009; Schafer et al., 1981; see also Costa-Faidella et al., 2011). Crucially, whatever the final explanation would be, both interpretations of our data (attenuation by the temporal preparation or enhancement in temporal mismatching conditions) are in accordance with the hypothesis that the brain uses rhythmic patterns to make predictions regarding the incoming target.

An alternative, but not incompatible, interpretation of the current findings concerns the repetition suppression phenomenon. Repetition suppression refers to the reduction of neural activity after the repetitive presentation of a stimulus (Grill-Spector, Henson, & Martin, 2006). This suppression of activity due to repetition would reflect an attenuation of surprise responses typically elicited by novel or unexpected sensory events. In this context, Costa-Faidella et al. (2011) showed that repetition suppression can be enhanced by temporal regularity (cf. Knolle, Schröger, Baess, & Kotz, 2011; see also Arnal and Giraud, 2012). These authors showed that the amplitude of the auditory N1 decreased as the number of stimulus repetitions was increased. Crucially, this N1 amplitude decrement by stimulus repetition was only obtained in isochronous sequences, as in our current experiment, and not in unpredictable sequences of tones. A recent study by Geiser et al. (Geiser, Notter, & Gabrieli, 2012) also supports the notion that temporal regularity results in the suppression of auditory neural activity. Using fMRI, these authors found less activation in the auditory primary cortex when the target was preceded by a regular rhythm as compared to an irregular rhythm. Taken together, these results are consistent with our findings, reinforcing the idea that the rhythms engaged temporal preparation about the exact moment of occurrence of the forthcoming stimulus.

Together with the N1 effect, we found that rhythms influenced the auditory P2 potential. In contrast to the N1, the P2 potential was enhanced at the foreperiod matching the rhythmic pace. While the N1 effect converged with previous research (e.g., Lange, 2009; Costa-Faidella et al., 2011), the auditory P2 enhancement was a novel and unexpected finding. In fact, Schafer et al. (1981) were the only to look at the auditory P2 in a related

study, finding an attenuation of this auditory evoked potential by regular rhythms in comparison to irregular rhythms (cf. Näätänen and Picton, 1987).

The lack of previous similar findings and a clear a priori hypothesis makes any interpretation of the P2 effect rather speculative. In fact, the scarce evidence existing in the literature in relation to the effect of temporal uncertainty on the auditory P2 potential reveals that temporal regularity typically leads to a decreased neural response rather than to an enhanced neural response (see Näätänen & Picton, 1987, for a review on this issue). One plausible interpretation relates the P2 enhancement to an endogenous attentional mechanism acting in our study. That is, although the rhythmic pace did not predict the moment of target appearance, participants would have used the rhythm as an explicit temporal cue, eliciting endogenous temporal orienting effects (e.g., Triviño et al., 2011), i.e., a fast rhythm acted as an early cue and a slow rhythm acted as a late cue. That way, while a bottom-up rhythmic entrainment would have resulted in an attenuation of the N1 potential, a top-down attentional process would have resulted in the enhancement of the late P2 potential (cf. Schmitd-Kassow, Schubotz, & Kotz, 2009). This is consistent with accounts reporting neural enhancement (rather than neural dampening) when predictive time occurs under the focus of explicit attention (see Arnal and Giraud, 2012; Lakatos, Karmos, Mehta, Ulbert, and Schroeder, 2008; Schroeder and Lakatos, 2009). At present, this interpretation remains to be confirmed by further research.

While the P2 enhancement reported here may have been produced by explicit attention, it is difficult to relate the N1 effect to endogenous temporal orienting for two reasons. First, our experiment was deliberately designed to avoid any influence of temporal orienting based on probabilistic cuing. Second, these results were opposite to the usual finding in

temporal orienting research, where potentials related to early perceptual processing are typically enhanced rather than attenuated, in both visual and auditory domains (Anderson & Sheinberg, 2008; Correa, Lupiáñez, et al., 2006; Lampar & Lange, 2011; Lange et al., 2006, 2003; Sanders & Astheimer, 2008; Seibold et al., 2011). Moreover, the conclusion that rhythms and temporal orienting effects involve dissociable mechanisms for temporal preparation is further supported by recent studies.

In a modification of the paradigm developed by Nobre and colleagues (Correa & Nobre, 2008; Doherty et al., 2005), it was found that temporal orienting was only effective when participants were instructed to attend to explicit visual temporal cues but not when they had to attend to a visual rhythm, whereas the regular rhythm improved behavioural performance independently of task instruction (Rohenkohl et al., 2011). Likewise, it has been reported that patients with lesions in the right prefrontal cortex were able to prepare on the basis of regular visual rhythms (Triviño et al., 2011), thus overcoming their deficit of temporal orienting based on predictive symbolic cues (Triviño et al., 2010). Rohenkohl and Nobre (2011) showed desynchronization of alpha-band oscillations driven by rhythms, peaking just prior to the onset of the expected target. A consequence of this attentional entrainment was the enhancement of neural activity related to visual perception. Note that the N1 amplitude effect reported here is also in line with entrainment models whereby rhythms produced temporal synchronization of attention with the regular pattern of stimuli (Large & Jones, 1999; Rohenkohl & Nobre, 2011; Schroeder & Lakatos, 2009). In our study, this entrainment would have produced the faster responses and the N1 effect at the intervals matching the rhythm temporal structure. Since in Rohenkohl et al.'s study the rhythms highly predicted the moment of target onset (i.e., a fast rhythm was associated in the 79% of the trials with an early onset

and a slow rhythm with a late onset), their results add to the extant literature showing perceptual enhancement by top-down temporal expectancies. The visual enhancement reported in Rohenkohl and Nobre's (2011) study contrasts with the auditory N1 attenuation reported in the present manuscript, which again supports dissociation between endogenous and exogenous temporal preparation. The question remains of whether the visual sensory enhancement found by Rohenkohl et al. was produced by the a priori probability manipulation between rhythms and foreperiods, by the attentional entrainment driven by the temporal structure of the rhythm, or both. Our findings of an attenuation of the N1 potential and an enhancement of the P2 potentials by rhythmic entrainment are in line with Rohenkohl and Nobre's and Lange's (2009) studies, suggesting the involvement of bottom-up and top-down attentional processes.

In sum, it will be interesting for future research to determine further the nature of the mechanism involved in rhythm-based temporal preparation. The current research suggests that this timing mechanism is proactive, that is, it uses the pace of temporal regularity provided by isochronous sequences of stimuli to predict (or reduce surprise to) forthcoming onsets of relevant events. As shown here, this mechanism is flexible because it can occur with multiple rhythmic paces. The effects of this temporal prediction include more efficient behavioural response to an auditory stimulus occurring at a moment matching the pace of a preceding rhythm, accompanied by the biases in early and late stages of auditory neural processing.

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## FOOTONE

1. A similar ANOVA was performed on the mean latency data with the values from the negative peak in that particular time window. This ANOVA a significant interaction between Rhythm and Foreperiod,  $F(1,11)=6.16$ ,  $p=.03$ , partial  $\eta^2=.35$ . Further comparisons revealed that the difference in latency of the N1 potential between both Rhythm conditions was marginally significant at the long Foreperiod,  $t(11)=2.10$ ,  $p=.06$ , with an earlier latency for the slow rhythm than for the fast rhythm (143 ms and 148 ms, respectively). The difference in latency between the fast (144 ms) and slow (147 ms) rhythms at the short foreperiod followed the expected trend but it did not reach statistical significance,  $t(11)=1.15$ ,  $p=.27$ . Neither the main effect of Rhythm nor the main effect of Foreperiod were significant, both  $F_s < 1$  (see Footnote 1). The ANOVA on the latency data of the P2 potential did not reveal any statistically significant effect (all  $F < 1$ ).

## FIGURE CAPTIONS

*Figure 1.* Schematic illustration of a trial.

*Figure 2.* Network of electrodes used in the present experiment. The electrodes included in the analysis are highlighted.

*Figure 3.* Mean RT in milliseconds ( $\pm$  standard error, S.E.) as a function of Rhythm (fast – 400 ms, slow – 900 ms) and Foreperiod duration (400, 900 ms).

*Figure 4.* Mean amplitude voltages ( $\mu$ V) over time in a representative electrode (7) showing the largest N1 potential as a function of Rhythm (fast, slow) at the 400-ms Foreperiod (top panel) and the 900-ms Foreperiod (bottom panel). The difference wave for the 400-ms foreperiod and the 900-ms foreperiod is also represented.

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Figure 1

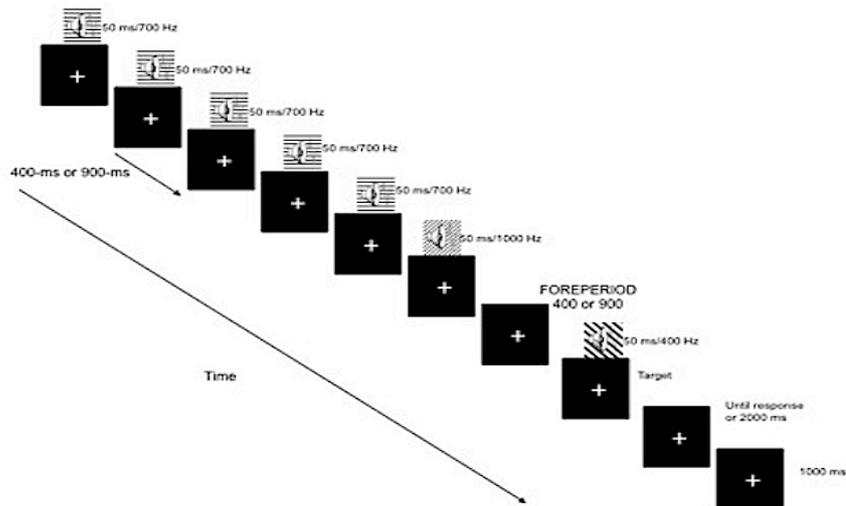


Figure 2

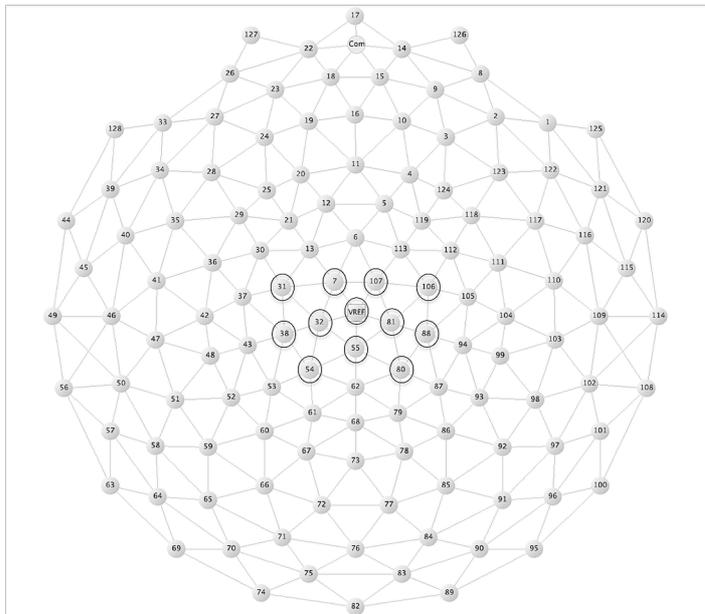


Figure 3

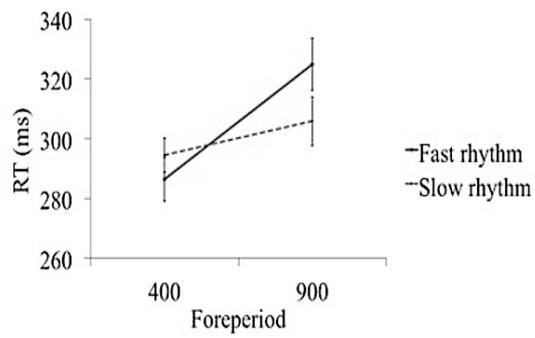


Figure 4

