Rhythmic temporal structure at encoding enhances recognition memory

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Abstract

Presenting events in a rhythm has been shown to enhance perception and facilitate responses for stimuli that appear in synchrony with the rhythm, but little is known about how rhythm during encoding influences later recognition. In this study, participants were presented with images of everyday objects in an encoding phase prior to a recognition task in which they judged whether or not objects were previously presented. Blockwise, object presentation during encoding followed either a rhythmic (constant, predictable) or arrhythmic (random, unpredictable) temporal structure, of which participants were unaware. Recognition was greater for items presented in a rhythmic relative to an arrhythmic manner. During encoding, there was a Dm effect with larger positivity for rhythmic over arrhythmic stimuli. At recognition, memory specific ERP components were differentially affected by temporal structure: the FN400 old/new effect was unaffected by rhythmic structure, whilst the late positive component (LPC) old/new effect was observed only for rhythmically encoded items. Taken together, this study provides new evidence that memory specific processing at recognition is affected by temporal structure at encoding.

1.0 Introduction

The influence of time has been observed in many different aspects of memory. Temporal experience not only provides structure to derive meaning from memory for sequences of events (Davachi & DuBrow, 2014), but also affects memory formation and dictates the likelihood that a particular piece of information will be remembered. For example, longer exposure durations lead to greater recognition of items compared to brief durations (Berry, Ward, & Shanks, 2017), and recognition is greater when the temporal order of events is held constant during encoding and retrieval (Hsieh & Ranganath, 2015; Tubridy, & Davachi, 2010). Moreover, the subjective duration with which items are presented is affected by their memory representation, for example, previously studied words are perceived to have been presented for a longer duration than new (non-studied) words (Ono & Kawahara, 2008; Whitherspoon & Allan, 1985). Hence, time and memory are fundamentally linked, yet relatively little is known about how temporal structure during encoding influences subsequent memory.

In recent years there has been a surge in interest in the way in which temporal expectation can shape perception and drive behaviour (see Nobre & van Ede, 2018, for a recent review). Temporal expectation generally refers to the anticipation that an event will occur at a particular point in time. Time, or temporal experience, is crucial to the formation of predictions of when an event will occur. The probability of an event occurring can change over time (e.g., based on the hazard function; Janssen & Shadlen, 2005; Luce, 1986), or be based on temporal associations such as knowing that a red traffic light will follow the amber. Expectations about when an event will occur can be driven by our goals, and the voluntary shifting of attention to a specific moment in time, which is associated with cognitive and behavioural gains. For example, using an informative cue has been shown to facilitate response times (RTs) (Griffin, Miniussi, & Nobre, 2001; Lange & Röder, 2006; Pomper, Keil, Foxe, & Senkowski, 2015), improve perceptual discrimination (Correa, Lupiáñez, & Tudela, 2005; Rohenkohl et al., 2014) and enhance neural processing for expected over unexpected targets (Buhusi & Meck, 2005; Correa, Lupianez, Madrid, & Tudela, 2006; Rohenkohl & Nobre, 2011; Zanto et al., 2011). However, temporal expectancies are not only driven by top-down processes but can be automatically shaped by events in our environment, such as the presence of a rhythm. Many everyday events follow a rhythmic pattern, such as walking, speech, and music.

There is mounting evidence that presenting stimuli in a rhythmic temporal structure can improve decision times (Jones et al., 2017; Martin et al., 2005), detection thresholds (Herrmann et al., 2016; Lawrance et al., 2014) and perceptual discrimination (Rohenkohl et al., 2012). According to the Dynamic Attending Theory (Large & Jones, 1999), rhythmic presentation generates peaks of attention focus, which leads to a processing advantage for items occurring at attended peaks.

Plainly, processing is optimal when items are presented in rhythm. Support for the DAT comes from pioneering work by Jones and colleagues (2002), who presented participants with two tones – a standard tone and a target tone –, and asked them to judge whether or not the two were of the same pitch. Sandwiched between the two tones were a series of additional tones, which formed a rhythm. Pitch judgement was best when target tones were presented in synchrony with the rhythm rather than out of synchrony; slightly early or late. Importantly, the rhythm *per se* did not carry any information beneficial to the pitch judgement task, but according to the DAT the rhythm created windows of heightened attention that served a processing advantage. Support for the DAT has also been observed in studies using event-related potentials (ERPs), where stimuli in synchrony with a rhythm demonstrate a larger amplitude for early perceptual components such as P1 (Rohenkohl & Nobre, 2011) and N1 (Escoffier et al., 2015). The enhancement of these components has, in selective spatial attention research, been associated with increased visual analysis of attended over unattended stimuli through a gain control mechanism (Hillyard & Annlo-Vento 1998; Luck et al., 2000). A concurrent line of research to the DAT is the idea that neuronal firing automatically entrains to external rhythms. Specifically, the phase of intrinsic brain oscillations entrain to ongoing external rhythms, aligning the firing pattern of neurons, and stimuli presented in phase with the oscillations are at a processing advantage compared to those presented out of phase (Arnal & Giraud, 2012; Lakatos et al., 2008; reviewed in Calderone et al., 2014; Henry & Herrmann, 2014).

Although there is growing evidence that rhythm provides a processing advantage leading to wide cognitive benefits (see Van Rullen, 2016; Haegens & Golumbic, 2017), the effect on long-term item memory is largely unexplored. It is well established that the way in which information is processed during encoding determines how efficiently memories are formed and later retrieved (Davachi & Dobbins, 2008). For example, the depth with which stimuli are processed during encoding affects subsequent retrieval (see Craik & Tulving, 1975; Craik, 2002), and object-focused attention (attending to particular items) during encoding leads to greater memory for attended than ignored items (e.g., Berry et al., 2010; Butler & Klein, 2009; Rees et al., 1999). It therefore seems intuitive that rhythm may bolster encoding to support memory. Recently, Clouter et al. (2017) showed that associative memory depends upon the timing synchrony between different sensory cortices at the theta frequency. In their study, memory for sound-movie clip pairs was greater when luminance and amplitude adjustments were synchronous rather than out of phase (see also Wang et al., 2018). The potential influence of rhythm on memory is further supported by observations that the hippocampus predominately oscillates at a theta frequency (Jacobs, 2014), and that specific neurons in the hippocampus are involved in the tracking of time (Kraus et al., 2013).

Thavabalasingam, O'Neil, Zeng, and Lee (2016) recently reported on the effect of temporal structure on recognition memory – the capacity to judge whether a specific item has been presented before in a particular context. Temporal structure was manipulated by varying the regularity of the inter-stimulus interval (ISI) in sequences of presentations of four items (ABCD). The sequences were repeated with fixed timings in the structured condition (e.g., A 100 ms; B 500 ms; C 1000 ms; D 2000 ms), and random timings in the unstructured condition. The presentation of items was fixed at 700 ms, as was the average length of the ISI, in the two conditions. Recognition was greater in the structured than the unstructured condition, and the effect occurred under both intentional encoding (Experiments 1 and 2) and incidental encoding (Experiment 3), and regardless of whether or not participants were aware of the temporal manipulation. It has also been shown that expecting a particular stimulus category during encoding enhances recognition (Bollinger et al., 2010; Bollinger et al., 2011). These studies provide evidence that expectancy generated through temporal structure is beneficial to recognition, but no prior study has directly examined the effect of temporal structure in the form of an isochronous rhythm or attempted to shed light on the underlying neural processes. The current study addresses this.

In this study participants were presented with a continuous stream of objects during encoding, under instructions to detect animals (targets) as quickly as possible. Across a series of blocks, the presentation onset of stimuli followed either an isochronous rhythmic temporal pattern or random and unpredictable timings. Importantly, the duration with which stimuli were presented, as well average trial length, was held constant in the two conditions. During the recognition phase participants judged whether individual items were previously presented during encoding (old) or not (new). Concurrently to the behavioural task electroencephalogram (EEG) was recorded to for the first time gain insight into the neural processes underlying any effect of rhythm on recognition. EEG was also used to examine the effects of temporal structure during encoding. This was assessed by determining the phase locking factor (PLF) (also referred to as inter-trial coherence, ITC), which was expected to be higher for rhythmic compared to arrhythmic stimuli. The effect of rhythm during encoding can also be observed by examining the ERPs. Based on the DAT we tested two separate, although not mutually exclusive, predictions. If increased temporal periods of attention affect perceptual processing of items then we would expect enhanced amplitudes for early components (P1 and N1). If the temporal manipulation leads to greater processing of rhythmic items, then we expect differences at later stages of processing. Specifically the *D*ifferential neural activity based on *m*emory (Dm) component, which has been proposed as one of the strongest indexes at the time of encoding of later successful retrieval (Paller & Wagner, 2002).

When comparing old and new test items, ERP studies have established two components related to recognition; the FN400 old/new effect and the parietal old/new effect, also known as the late positive component (LPC) (Duarte et al., 2004; Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran 2007; Voss et al., 2010; Woodruff et al., 2006). The FN400 is a negative component around 300-500 ms over frontal areas, and the LPC a positive deflection over parietal electrodes. A number of studies have associated the FN400 old/new effect with the process of familiarity (Curran, 2000; Curran & Cleary, 2003; Curran & Doyle, 2011; Duarte et al., 2004; Düzel et al., 1997; Ecker et al., 2007; Groh-Bordin et al., 2006; Rugg & Curran, 2007; Smith, 1993, but see Olichney et al., 2000; Tsivilis et al., 2001) and the LPC with recollection (Allan, Wilding, & Rugg, 1998; Curran, 1999, 2000; Curran & Cleary, 2003; Griffin et al., 2013; Duarte et al., 2004; Rugg & Curran 2007; Voss et al., 2010; Woodruff et al., 2006, but see Finnigan et al., 2002). Alternatively, these two memory specific components may reflect differences in the strength of the encoded representation (e.g., Brezis et al., 2017). For example, deeper processing (e.g., conceptual rather than perceptual) has been associated with increased LPC old/new effect, whilst the FN400 has shown to be unaffected by depth of processing (Rugg et al., 1998).

We predicted a facilitation in the encoding of objects presented in a rhythmic relative to an arrhythmic manner, leading to greater recognition in the former condition. Moreover, if rhythm boosts encoding, leading to stronger, deeper memory representations than arrhythmic encoding, then we would expect the FN400 and LPC old/new recognition ERP components to interact with temporal structure. To foreshow the results, recognition was significantly greater following rhythmic than arrhythmic encoding, and the LPC old/new effect was present for rhythmically encoded items only.

2.0 Method

2.1 Participants and Design

Twenty-four students (9 male, mean age = 23.3 years, *SD* = 2.4 years) from Middlesex University, London, took part in exchange for a £20 gift voucher. All were fluent in English language with normal or corrected vision, and 22 were right handed. Ethical approval was granted by the Middlesex University Research Ethics Committee, and all participants provided written informed consent. One participant was removed prior to analysis as they failed to follow the instruction to detect targets during encoding (detection tasks, see Procedure).

The experiment involved the within-participants comparison of the effect of temporal structure (rhythmic versus arrhythmic) on recognition memory. Each participant was exposed to three encoding-test blocks in each condition, and the order of blocks was counterbalanced, such that half of the participants performed the blocks in the following order: rhythmic 1 – arrhythmic 1 – rhythmic 2 – arrhythmic 2 – rhythmic 3 – arrhythmic 3, and the other half in the reverse order: arrhythmic 1 – rhythmic 1 – arrhythmic 2 – rhythmic 2 – arrhythmic 3 – rhythmic 3.

2.2 Stimuli

The stimuli were 480 400 x 400 pixel greyscale images of familiar everyday objects (e.g., a car, a chair). Each of the six encoding phases contained a unique set of 40 images, randomly interspersed among 120 presentations of a 400 x 400 pixel checkerboard (Figure 1), resulting in a ratio of 3:1 checkerboard to stimulus presentations. The test phase within each block contained the 40 items from the encoding phase immediately prior, and 40 new items. Items were counterbalanced between participants such that each set of 40 images appeared an equal number of times in each block, and an equal number of times as studied (old) or new type. Target items in the encoding phases (the detection task, see Procedure) were images of animals. There were four targets in each encoding block, 24 in total across the experiment (10% of encoding phase trials). An equal proportion of previously studied and new images of animals were presented at test (i.e., 4 old and 4 new in each block).

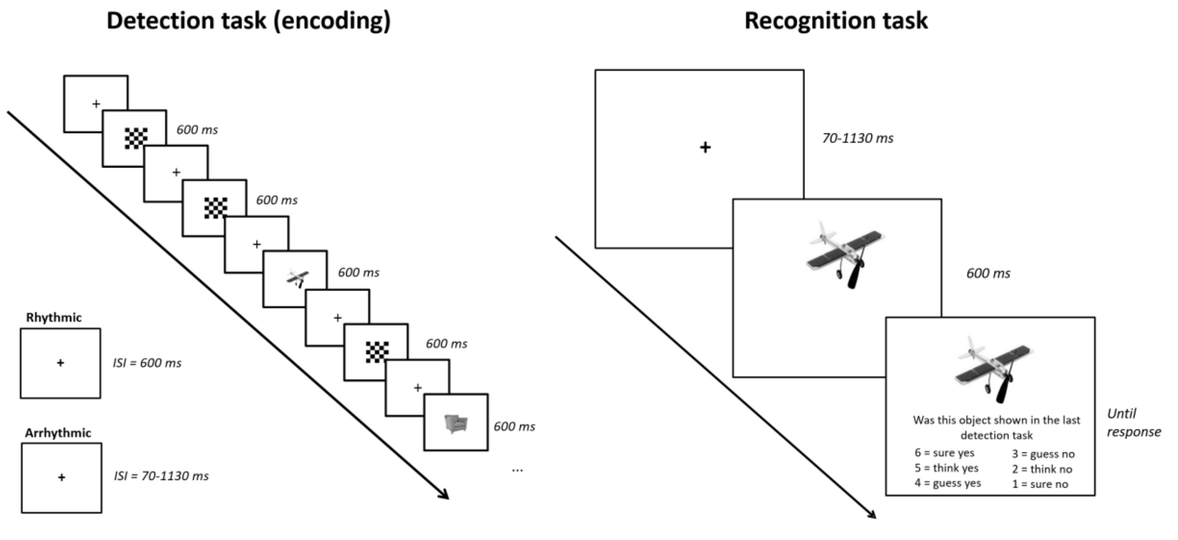

Figure 1 (Left): Events in the Detection Task within each block. Objects and checkerboards were presented for a fixed duration of 600 ms in the Rhythmic and Arrhythmic conditions. The ISI (fixation point) was presented for 600 ms in the Rhythmic condition, and in the Arrhythmic condition was presented for an interval randomly generated from a uniform distribution with a range of 70 ms to 1130 ms and a mean of 600 ms. **Right:** Schematic representation of the events in the recognition task. Each item (old or new object) was presented for 600 ms after which time the participant had to respond whether or not they had seen the item before.

2.3 Procedure

The experimental task was programmed in Matlab 2013a, and performed on a PC with a screen resolution of 1280 x 1024 pixels in sound attenuated cubicle. Participants were tested individually and the duration of the experiment was approximately one hour (not including EEG preparation).

Participants were informed that the experiment consisted of six blocks, each with two separate tasks: a detection task, and a memory task. In the detection task (encoding phase), participants were told that they would see a series of images of objects and checkerboards in rapid succession on the computer screen and that their task was to press the spacebar as quickly as possible whenever they saw an animal. They were informed that animals would be presented on approximately 10% of trials, and that the majority of images would be checkerboards. A ratio of 3:1 checkerboards to objects was used to extend the duration of the encoding phase, to create a maximally rhythmic or arrhythmic sense of presentation, and at least one checkerboard was presented between any two objects. Participants were informed that their memory for the items presented in each detection task would be tested afterwards, but they were not informed of the temporal structure manipulation. Each trial in the detection task consisted of a black central fixation point on a white screen, followed by an image of an object or checkerboard in the centre of the screen (Figure 1). The fixation point was presented during the ISI, and the duration differed in the rhythmic and arrhythmic blocks. In the three rhythmic blocks, the ISI was held constant at 600 ms, generating a rhythmic presentation of stimuli at 1.67Hz. In the three arrhythmic blocks, the ISI duration was randomly generated from a normal distribution with a range of 70 ms to 1130 ms and a mean of 600 ms. In all blocks (rhythmic and arrhythmic) objects and checkerboards were presented for precisely 600 ms. Thus, all events in the rhythmic condition were constant and predictable, and although the duration with which objects and checkerboards were presented was equivalent in the rhythmic and arrhythmic blocks, stimulus onset was not predictable in the arrhythmic blocks. Each detection task included 160 randomised trials (40 objects and 120 checkerboards), plus an additional ten checkerboards at the start of the phase prior to experimental trials. Importantly, the total duration of the detection task in each block was equivalent. Accuracy and speed of spacebar presses was recorded.

Following the detection task, participants solved simple algorithmic problems for three minutes prior to the recognition task. Participants were aware that their memory for the items presented in each block would be tested (given the blocked design, incidental encoding was not possible). The recognition task within each block included the 40 objects from the detection task immediately prior, along with 40 new items, in a new random order for each participant. On each trial, an object was presented in the center of the screen for 600 ms, after which time the instruction "*Was this object shown in the last detection task?*", and the response scale "*6 = sure yes, 5 = think yes, 4 = guess yes, 3 = guess no, 2 = think no, 1 = sure* no" appeared below the object. Participants were required to indicate their response via a number keypress. In order to encourage participants to respond "yes" or "no" roughly equally, they were informed that half of the items in each memory task were new and half were shown in the prior detection task. No time limit was imposed, and the object and response scale remained on the screen until a keypress was made. A central fixation point was presented for a random duration ranging between 70–1130 ms prior to the next trial.

At the start of the experiment participants performed two short practice blocks including eight detection trials and 16 recognition trials (half studied and half new). The detection task in the first practice block involved rhythmic timings, and the second involved arrhythmic timings. After this, participants completed the six experimental blocks, with a 5-min break between the third and the fourth blocks. On completion, participants were probed for awareness of the rhythmic versus arrhythmic presentation of images in the different blocks. They were initially asked whether they noticed any difference in the detection task between blocks, and if so, to explain it. Participants who correctly identified the manipulation were asked whether they became aware during the task or in hindsight.

2.4 EEG Recording and Analysis

Electroencephalography (EEG; BioSemi Active Two system) was recorded from 64 locations on the scalp throughout the experiment (both encoding and recognition) with a sample rate of 2048Hz and reference to the CMS-DRL (common mode sense-driven right leg). Horizontal electro-oculogram (HEOG) was recorded from the outer canthi of the eyes. Off line data analysis (Brain Vision Analyzer v2.1.1, Brain Products GmbH) included down sampling the data to 1000 Hz. Bad channels were interpolated and these were identified manually, on a participant-by-participant basis, by raw-data inspecting. No channels included in the data analyses (Fz, P3, PO7or PO8) were interpolated. A second order Butterworth zero-phase band-pass filter with low cut-off of 0.1 Hz and a high cut-off of 40 Hz, and a 50 Hz zero-phase notch filter were applied to each participant's continuous data. Data were then re-referenced to the average of all 64 electrodes. Eye-blinks and horizontal eye-movements were corrected in a semi-automatic mode, using ocular correction independent component analysis (ocular correction ICA, Brain Vision Analyzer). ERPs were epoched into 900 ms segments ranging from 100 ms pre-stimulus onset to 800 ms post-stimulus onset. A 100 ms pre-stimulus baseline correction was performed on each ERP by subtracting the mean voltage in that interval from every voltage point (1 / ms) in the ERP. Artefact rejection was performed on all channels excluding segments with amplitudes than ±100 µV.

2.4.1 Detection task analysis:[1]

2.4.1.1 ERPs:

Objects and checkerboard items were averaged separately for the rhythmic and arrhythmic conditions. The P1 (102-142 ms) and N1 (146-206 ms) intervals were peak centred (122 ms, and 176 ms averaged at PO7/8 across all conditions). The P1 and N1 analyses were centred on the occipital-parietal PO7 and PO8 where effects of attention have previously been reported (Doherty, Rao, Mesulam, & Nobre, 2005; Griffin, Miniussi, & Nobre, 2002). Both the P1 and N1 have been shown to be modulated by temporal expectancies (see Correa et al., 2006 for a review). The *'Dm'* (400-800 ms) effect ('differences due to subsequent memory') was measured at posterior electrodes (PO7/8) in the 400-800 ms interval (Paller & Wagner, 2002). The Dm effect typically refers to a comparison between hits and misses. Due to a low number of misses (see footnote 1) the Dm analysis here is a comparison between rhythmic and arrhythmic mean amplitudes in the 400-800 ms time interval. Each time interval was analysed with a 2x2x2 repeated measures ANOVA with the factors; Temporal structure (rhythmic, arrhythmic), Electrode (PO7, PO8), and Object type (object, checkerboard).

2.4.1.2 Phase locking factor analysis:

To investigate the phase locking factor (PLF, aka inter-trial coherence) during encoding the EEG data was segmented into 2000 ms segments, 1000 ms before and 1000 ms after stimulus onset. The data were segmented separately for objects and checkerboards in the rhythmic and arrhythmic encoding conditions. The following pre-processing steps were identical to those described above; filtering, re-referencing, ICA correction and topographical interpolation. A 100 ms pre-stimulus baseline correction was used and artefact rejection was performed on all channels, excluding segments with amplitudes than ±100 µV in the -200 to 600 ms time interval. The rejected segments were marked as bad segments and the markers were re-imported so the following analysis could be performed on non-baseline corrected data. A complex Morlet wavelets (Morlet parameter c=3) analysis was conducted on each segment and one layer was transformed with a central frequency of 1.67 Hz (1.21-2.13 Hz). The phase locking factor across trials was computed for each time point for electrodes PO7 and PO8. The electrode choice was based on what has previously been used to

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[1] Initially we planned to compare ERPs for hits versus misses in the encoding data. However, the average number of misses was low, with 14.22 (SD 10.15) trials in the rhythmic and 17.70 (SD 15.12) in the arrhythmic encoding condition. The trial numbers were therefore too low to perform a reliable ERP analysis.

investigate the phase locking using visual stimuli (e.g., Cravo, Rohenkohl, Wyart, & Nobre, 2013). To avoid stimulus onset artefacts, an average value was computed 200 ms before stimulus onset and used for analysis (Notbohm & Herrmann, 2016). The PLF was submitted to a 2x2x2 repeated measures ANOVA with Object type (checkerboards, objects), Temporal structure (rhythmic, arrhythmic) and Electrode (PO7, PO8).

2.4.2 Recognition task analysis:

Average ERPs were computed for each participant in the rhythmic and arrhythmic conditions, separately for hits, misses, correct rejections, and false alarms. Mean amplitudes were compared for hits (old) and correct rejections (CR; new) at mid-frontal electrode Fz in the 300-500 ms interval, for FN400 and for the LPC the left-parietal electrode P3 was selected in the 500-800 ms interval. The electrode choice and time intervals are based upon a large body of research (see Rugg & Curran, 2007, for a review) and are identical to recent studies such as Bergstrom et al. (2016). For each interval, mean amplitudes were submitted to a 2x2 repeated measures analysis of variance (ANOVA) with the factors Item (old, new) and Temporal structure (arrhythmic, rhythmic).

3.0 Results

3.1 Behavioral Results

An alpha level of .05 was used for all statistical tests, and *t* tests are two-tailed. Where the assumption of sphericity is violated, Greenhouse-Geisser adjusted degrees of freedom and probability levels are reported.

3.1.1 Detection task:

The number of targets correctly detected, the associated mean RT, and the number of erroneous keypresses (to non-targets) was computed, collapsed across the rhythmic and arrhythmic blocks (Table 1). Correct detection of targets, and erroneous keypresses to non-targets did not significantly differ between the rhythmic and arrhythmic conditions (*t*(22) = 1.10, *p* = .283, *d* = 0.30, and *t*(22) = 0.36, *p* = .723, *d* = 0.10, respectively). However, participants were significantly faster in detecting targets in the rhythmic than the arrhythmic condition (*t*(22) = 2.43, *p* = .024, *d* = 0.56).

Table 1. *Performance in the Detection Task collapsed across the Rhythmic and Arrhythmic blocks.*

	Rhythmic *M* (*SD*)	Arrhythmic *M* (*SD*)	
Correct Detection of Targets (%)	97.46 (3.92)	95.29 (9.34)	ns
Erroneous Responses (%)	0.76 (0.77)	0.68 (0.80)	ns
RT (correct)	485 (70)	526 (78)	$p = .024$

3.1.2 Recognition task:

Across blocks, ratings 1–3 and 4–6 on the scale were collapsed into '*no*' (non-studied, new) and '*yes*' (studied, old) responses, respectively. The response scale was used to capture a broad range of yes and no responses, but responses were not analysed according to confidence since this was not directly relevant to our aim and there were too few trials within intervals. Corrected recognition was calculated as the proportion of hits ('*yes*' responses to studied items) minus false alarms ('*yes*' responses to new items). See Table 2 for proportions of hits, false alarms, misses ('*no*' judgments to previously studied items), and correct rejections ('*no*' judgments to new items), and Figure 2 for corrected recognition collapsed across the rhythmic and arrhythmic blocks.

Collapsed across block, performance was significantly greater than chance in both the rhythmic condition ($t(22) = 33.77$, $p < .001$, $d = 7.04$) and the arrhythmic condition ($t(22) = 24.00$, $p < .001$, $d = 5.01$). Recognition was significantly greater in the rhythmic condition than the arrhythmic condition ($t(22) = 2.29$, $p = .032$, $d = 0.30$). To examine possible variation of recognition accuracy across blocks, a repeated measures ANOVA was performed, indicating no significant main effect of block ($F(3.17, 66.88) = 1.23$, $p = .308$, $\eta_p^2 = .06$), no significant main effect of the counterbalanced order of blocks ($F(1, 21) = 1.91$, $p = .181$, $\eta_p^2 = .08$), and no significant interaction ($F(5, 105) = 1.02$, $p = .409$, $\eta_p^2 = .06$).

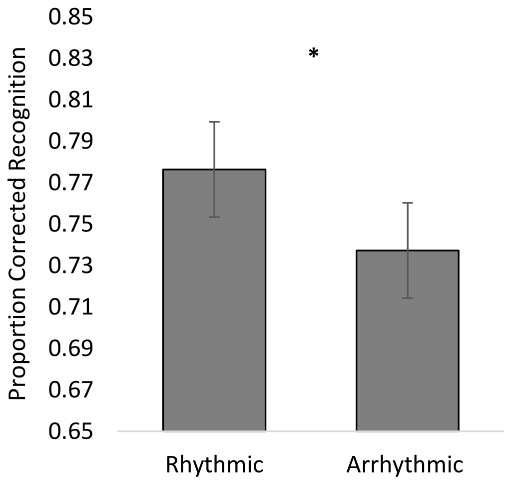

Figure 2. Corrected Recognition in the Rhythmic and Arrhythmic conditions, collapsed across block. Error bars indicate Standard Error of the Mean.

Collapsed across block, overall mean RTs for recognition judgments did not differ in the rhythmic condition (*M* = 968 ms; *SD* = 559 ms) and the arrhythmic condition (*M* = 974 ms, *SD* = 515 ms)($t(22) = 0.16$, $p = .873$, $d = 0.01$). RTs were analysed according to whether the recognition response was a hit, miss, false alarm (FA), or correct rejection (CR) (Table 2). There was a significant main effect of recognition response on RT in the rhythmic condition ($F(2.09, 45.99) = 19.25$, $p < .001$, $\eta_p^2 = .48$) and the arrhythmic condition ($F(2.25, 49.57) = 40.33$, $p < .001$, $\eta_p^2 = .65$). RTs for hits were faster than RTs for all other responses in both conditions (all *t*'s > 2, *p*'s < .025), and CR were made significantly faster than FA and misses in both conditions (all *t*'s > 4, *p*'s < .001). The only nonsignificant comparison was between FA and misses ($p > .05$ in both conditions).

Only 3/23 participants reported awareness that presentation timings in the detection task varied across blocks, thus no reliable comparison with the performance of unaware participants was possible, but collapsed recognition scores in aware participants were similar to the group means (.79 and .72 in the rhythmic and arrhythmic conditions, respectively).

Table 2. *Top panel: Proportions of Hits, Misses, False Alarms, and Correct Rejections in the Recognition Task collapsed across the Rhythmic and Arrhythmic blocks. Bottom panel: Response Times (RT) in milliseconds by Recognition Response.*

	Rhythmic *M* (*SD*)	Arrhythmic *M* (*SD*)
Hits	0.88 (0.08)	0.85 (0.13)
Misses	0.11 (0.09)	0.86 (0.20)
False Alarms	0.11 (0.07)	0.11 (0.07)
Correct Rejections	0.14 (0.13)	0.85 (0.19)
RT Hits	789 (493)	801 (471)
RT Misses	1638 (916)	1569 (705)
RT False Alarms	1667 (987)	1779 (806)
RT Correct Rejections	1006 (593)	939 (468)

3.2 EEG Results

In short, there was an N1 effect of Temporal structure for checkerboards but not for objects. There was also a Dm temporal structure effect for both objects and checkerboards with larger positivity for rhythmic compared to arrhythmic items (Figure 3). Moreover, overall, there was greater Dm positivity for objects compared to checkerboards. In the recognition phase, there was an FN400 old/new effect for both rhythmic and arrhythmic items whilst a LPC old/new effect only for rhythmic items. Finally, the two ERP effects of Temporal structure at encoding significantly correlated with the behavioural effect of temporal structure at recognition.

3.2.1 Detection task:

ERPs

P1 (102-142 ms)

There was a main effect of Electrode (*F*(1,22)= 7.16, *p* = .014, η_p^2 .245) with higher amplitude for PO7 (*M* 3.25 µV *SEM* 0.45) compared to PO8 (*M* 2.44 µV, *SEM* .48 µV). There was no main effect of Object type (*p* = .214, η_p^2 .069) or Temporal structure (*p*=.633, η_p^2 .011). No Electrode*Object type (*p* = .166, η_p^2 .085) or Electrode*Temporal structure interaction (*p* = .146, η_p^2 .093), or Electrode*Object type*Temporal structure interaction (*p* = .557, η_p^2 .016). There was a significant Object type*Temporal structure interaction (*F*(1,22)= 4.39, *p* = .048, η_p^2 .166). Separate follow up analysis for each Object type (Bonferroni adjusted; alpha = .025) showed no effect of Temporal structure for checkerboards (*p* = .103, η_p^2 .116, BF_{10} = 0.31, 0.92% error) [2] or objects (*p* = .364, η_p^2 .038, BF_{10} = 0.24, 0.93% error). Moreover, there was no effect of Object type for rhythmic (*p* = .082, η_p^2 .131) or arrhythmic items (*p* = .712, η_p^2 .006). Taken together the P1 was not affected by Temporal structure or differed significantly for objects and checkerboards.

N1 (146-206 ms)

There were no main effects of Object type (*p* = .061, η_p^2 .150), Temporal structure (*p*=.063, η_p^2 = .148) or Electrode (p=.193, η_p^2 .076). No significant Electrode*Object type (*p* = .246, η_p^2 .061), Electrode*Temporal structure interaction (*p* = .143, η_p^2 .095) or Electrode*Object type*Temporal structure interaction (*p* = .760, η_p^2 .004). However, there was a significant Object type*Temporal structure interaction (*F*(1,22)= 4.64, *p* = .042, η_p^2 .174).

Follow-up analysis (Bonferroni adjusted; alpha = .025) showed an effect of Temporal structure for checkerboards (*F*(1,22)= 6.56, *p* = .018, η_p^2 .230) with overall larger positive amplitude for rhythmic (*M* 1.69 µV, *SEM* .34 µV) compared to arrhythmic checkerboards (*M* 1.27 µV, *SEM* .27

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[2] Bayes Factor analysis (JASP Team (2017) (JASP (Version 0.9.2)[Computer software]) was conducted for null effects including Temporal structure which were directly related to our hypotheses and subsequently interpreted. A (BF_{10}) value of less than 1/3 is considered as support the null hypothesis compared to the theory (Dienes, 2014).

µV). In relation to the N1 component, this effect can be viewed as larger N1 for arrhythmic compared to rhythmic checkerboards. There was no effect of Temporal structure for objects only (p = .738, η_p^2 = .005, BF_{10} = 0.23, 0.03% error). Separate analysis of rhythmic and arrhythmic items showed no effect of Object type (p = .033, η_p^2 = .191; and p = .131, η_p^2 = .101, respectively).

Phase locking factor (PLF)

There was a significant main effect of Temporal structure ($F(1, 22)$ = 14.83, p = .001, η_p^2 =.40) with a higher PLF in the rhythmic (*M* 0.26, *SEM* 0.02) compared to the arrhythmic condition (*M* 0.20, *SEM* 0.01). There was no main effect of Object type (p = .686, η_p^2 = .008) Electrode (p = .393, η_p^2 = .033) or Temporal structure*Electrode (p = .374, η_p^2 = .036), Object type*Temporal structure (p = .071, η_p^2 = .141), Object type*Electrode (p = .080, η_p^2 = .133), Object type*Electrode*Temporal structure interaction (p = .971, η_p^2 = .001).

3.2.2. Dm effect (400-800 ms)[3]

There was an effect of Temporal structure ($F(1,22)$= 5.86, p = .024, η_p^2 = .210) with overall larger positive amplitude for rhythmic (*M* 1.59 µV, *SEM* .23 µV) compared to arrhythmic items (*M* 1.24 µV, *SEM* .20 µV). There was also a main effect of Object type ($F(1,22)$= 17.96, $p < .001$, η_p^2 = .449) with overall larger positive amplitude for objects (*M* 1.96 µV, *SEM* .27 µV) compared to checkerboards (*M* 0.87 µV, *SEM* .20 µV). There was no effect of Electrode (p = .053, η_p^2 = .160) or two-way interactions between Electrode*Object type (p = .098, η_p^2 = .119), Temporal structure*Electrode (p = .684, η_p^2 = .008), Temporal structure*Object type (p = .326, η_p^2 = .044) or three-way interaction (p = .931, η_p^2 = .001).

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[3] As it is possible that the next stimulus could be presented in the 670-800 ms interval in the arrhythmic condition due to the random ISI, the Dm effect was also analysed for the 400-670 ms time interval. Similarly to the 400-800 ms analysis, there was a main effect of Temporal structure ($F(1, 22)$ = 5.14, p = .034, η_p^2 =.189) with larger positive amplitude for rhythmic (*M* 1.82 µV, *SEM* .25 µV) compared to arrhythmic items (*M* 1.49 µV, *SEM* .21 µV). That is, there was a Dm effect also in the 400-670 ms interval. This analysis also showed an effect of Electrode ($F(1, 22)$ = 4.70, p = .041, η_p^2 =.176) and Item type ($F(1, 22)$ = 37.49, $p < .001$, η_p^2 =.630). There was no Electrode*Item type (p = .063, η_p^2 =.148), Electrode*Temporal structure (p = .608, η_p^2 =.012), Temporal structure*Item type (p = .386, η_p^2 =.034) or Temporal structure*Item type*Electrode interaction (p = .694, η_p^2 =.007).

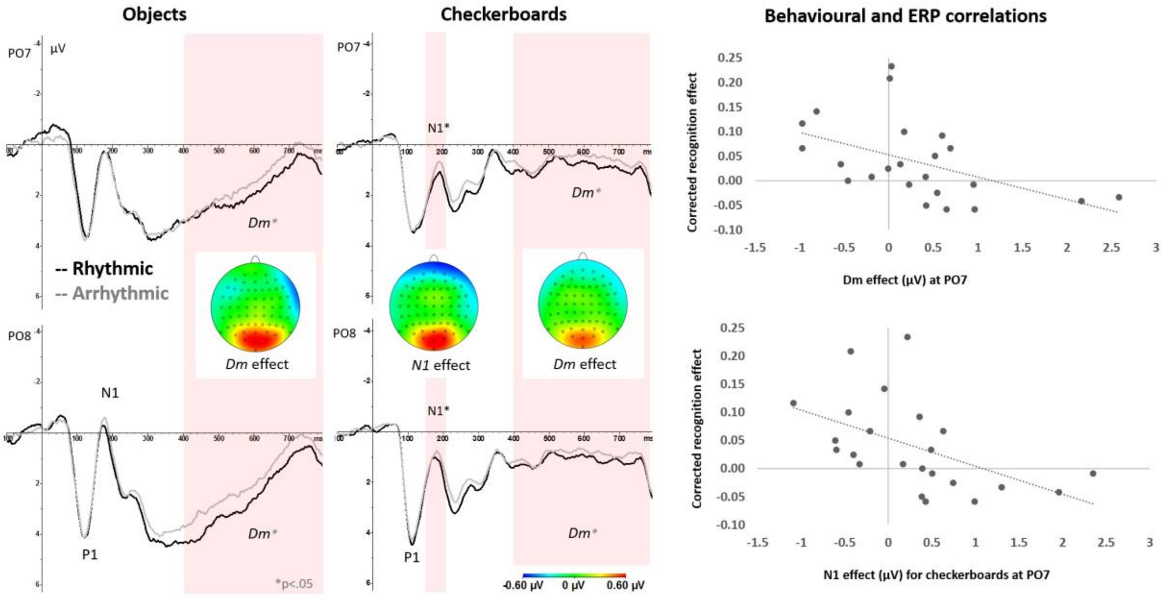

Figure 3. Grand averaged ERPs time locked to item onset (0 ms) of the objects (**Left**) and checkerboards (**Middle**) in the rhythmic (black) and arrhythmic (grey) conditions during the encoding phase. ERPs are presented for electrodes PO7 (top) and PO8 (bottom) used for analysis. Shaded areas represent significant difference between rhythmic and arrhythmic conditions. The topographical maps show the effect of temporal structure (rhythmic minus arrhythmic) in the N1 interval (146-206 ms; checkerboards only) and the Dm time interval (400-800 ms). X-axis is time (in milliseconds) and y-axis represents ERP amplitude (in microvolts - µV). **Right**: Scatterplots of the significant correlation between the behavioural recognition effect (rhythmic–arrhythmic corrected recognition) (y-axis) and the ERP effects at PO7 (rhythmic – arrhythmic ERP amplitude) (x-axis). Top scatterplot represents the correlation between behavioural and Dm effect (averaged effect over objects and checkerboards). Bottom scatterplot shows the relationship between behavioural and N1 effects for checkerboards.

3.2.2 Recognition task:

ERPs

A 2x2 repeated measures ANOVA with the factors Temporal structure (arrhythmic, rhythmic) and Item (old, new) was used for each time interval.

FN400 (300-500 ms, Fz electrode)

There was a main effect of Item ($F(1, 22) = 16.06$, $p = .001$, $\eta_p^2 = .42$) over Fz with old items showing larger positive amplitude (*M*-1.03 µV, *SEM* .25 µV) compared to new items (*M* -1.44 µV, *SEM* .25 µV) (Figure 4). There was no effect of Temporal structure ($p = .666$, $\eta_p^2 = .009$, $BF_{10} = 0.24$, 0.034% error) nor Temporal structure*Item interaction ($p = .405$, $\eta_p^2 = .03$). In other words, the FN400 showed an old/new effect.

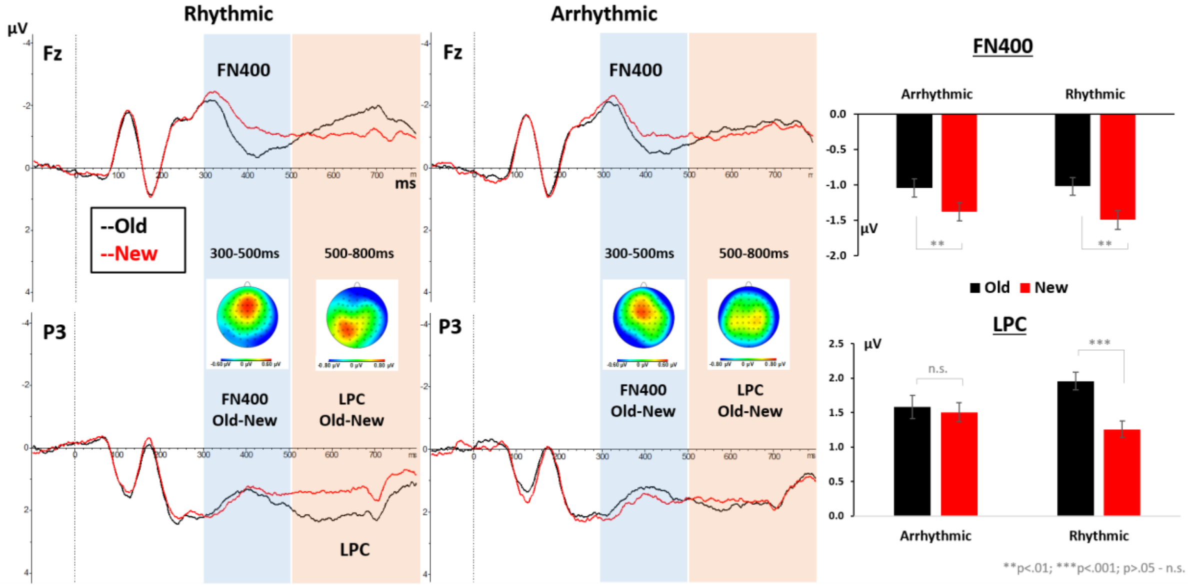

Figure 4. ***(Left and middle)*****:** Grand average ERP waveforms for old/hits (black) and new/CR (red) items during the recognition phase, presented separately for items which were presented during the rhythmic and arrhythmic temporal encoding structure. Y-axis is ERP amplitude (microvolts) and x-axis represents time with 0 ms being the onset of the item. Top row shows Fz electrodes used to analyse the FN400 in the 300-500 ms interval (blue shaded area). The bottom row shows P3 electrodes included in the LPC analysis in the 500-800 ms time interval. **Right (top):** Average ERP amplitudes in the 300-500 ms interval at electrode Fz for old (black) and new (red) trials. The asterisks represent the significant main effect of Item at the FN400. **Right (bottom):** Average ERP amplitudes in the 500-800 ms interval plotted for electrode P3. This bar graph shows the interaction with an observed LPC in the rhythmic but not arrhythmic encoding conditions.

Late Positive Component (LPC, 500-800 ms, P3 electrode)

There was no main effect of Temporal structure (p = .519, η_p^2 .02) or Item (p = .055, η_p^2 .16), whilst there was a significant Temporal structure*Item interaction (F(1, 22) = 4.53, p = .045, η_p^2 .17). Follow-up analyses for Rhythmic items only showed a significant difference between Old (M 1.96 µV, *SEM* .28) µV) vs New (M 1.23 µV, *SEM* .24 µV) items (t(22) = 4.40, p < .001, d= 0.58), whilst no difference between old and new items when presented during arrhythmic encoding (p = .970, BF_{10}=0.23). Moreover, post-hoc tests comparing Arrhythmic Hits vs. Rhythmic Old items was non-significant (p = .061, BF_{10}= 1.12) as was Arrhythmic New items vs Rhythmic New (p = .128, BF_{10} = 0.65.

3.3 Correlations.

To correlate effects at encoding with retrieval, new variables were computed. An average behavioural effect was calculated by subtracting rhythmic – arrhythmic corrected recognition scores for each participant. The N1 ERP effect of Temporal structure was calculated by taking rhythmic – arrhythmic mean amplitudes for the checkerboards only in the 146-206 ms interval separately for PO7 and PO8. The effect in the Dm interval was calculated the same way except the effect is averaged across both objects and checkerboards (correlations for the two electrodes were Bonferroni adjusted; alpha = .025). There was a significant correlation between the checkerboard N1 effect at PO7 and behaviour (*r* = -.507, *p* =.014) but not at PO8 (*r* = -.383, p=.071). Moreover, there was also a significant correlation between the Dm effect and behavioural recognition at PO7 (*r* = -.490, *p* =.018) and not PO8 (*r* = -.334, *p* =.120) (Figure 3, right). To note is that the significant correlations are negative, which is opposite to what would be expected. The larger behavioural effect is associated with a smaller ERP effects at encoding. A PLF effect variable of Temporal structure was similarly computed by averaging across objects and checkerboards, separately for PO7 and PO8, then taking rhythmic – arrhythmic PLF values to generate a PLF effect. There were no correlations of PLF effect and behavioural effect at either PO7 or PO8 (*r* =.-060, *p* =.785; and *r* =.078, *p* =.724, respectively).

4.0 Discussion

This study provides novel evidence that rhythmic encoding is beneficial to recognition and is associated with distinct neural processes as compared to arrhythmic encoding. Participants were exposed to six encoding-test blocks, three in which the interval between items presented at encoding was fixed (rhythmic), and three in which the interval was randomly varied – an arrhythmic condition. Although participants were largely unaware of the temporal manipulation, recognition was superior for items studied in a rhythmic relative to an arrhythmic manner. Moreover, temporal structure during encoding modulated memory specific ERP components at retrieval: the FN400 old/new effect was present in both the rhythmic and arrhythmic conditions, but a late positive component (LPC) old/new effect was observed only for rhythmically encoded items. This suggests that temporal structure influences processing during encoding to benefit subsequent memory.

The temporal manipulation may have increased expectancies in the rhythmic condition. Temporal expectations can be generated in different ways, such as by informative associations between events, by varying the probability of when an event will occur, or the presence of a pattern or rhythm, and these expectations can be generated automatically or voluntarily (Nobre & van Ede, 2018). Such temporal expectation has previously been shown to provide a benefit to memory, and the behavioural findings reported here are in line with the study by Thavabalasingam et al. (2016), who manipulated temporal structure by presenting stimuli in a fixed repeating sequence of presentation timings (i.e., 100 ms; 500 ms; 1000 ms; 2000 ms). In their study the presentation of items in the sequence condition was predictive, meaning that participants were able to learn to expect items to be presented at particular points in time, and they reported greater recognition for items presented in sequence relative to those with random onset timings.

The rhythmic or synchronous presentation of stimuli has a direct benefit on decision times (Martin et al., 2005), detection thresholds (Herrmann et al., 2016; Lawrance et al., 2014), and perceptual discrimination (Rohenkohl et al., 2012), however, to our knowledge the current study is the first to examine the specific effect of rhythmic encoding on recognition and the underlying neural processes. Clouter et al. (2017) recently showed that synchronising rhythmic input between auditory and visual stimuli improves associative memory. They found the synchronising effect at the theta frequency (4 Hz), matching the intrinsic frequency of the hippocampus (Jacobs, 2014), whilst no effect at delta (1.7 Hz) or alpha (10.5 Hz) was observed. They concluded that episodic memory formation in humans relies on a theta-specific synchronization mechanism. The rhythmic frequency in the present study matched their slower control frequency where they found no effect. Although the tasks and memory processes are different in the two studies, the present findings show that rhythmic temporal structure can provide a benefit to memory outside of the theta frequency range.

One theoretical explanation for greater recognition in the rhythmic compared to the arrhythmic condition concerns the Dynamic Attending Theory (DAT; Large & Jones, 1999). The DAT is not restricted to any specific frequency but suggests that rhythms automatically entrain peaks of attention focus with a processing advantage for stimuli presented in time with the rhythm. In a similar framework, the advantage for rhythmically presented items can be explained through the notion that intrinsic brain oscillations entrain to ongoing external rhythms, aligning the firing pattern of neurons such that stimuli presented in phase are at a processing advantage compared to those presented out of phase (Arnal & Giraud, 2012; Lakatos et al., 2008; reviewed in Calderone et al., 2014; Henry & Herrmann, 2014). To investigate the underlying processing of rhythmic input, the present encoding data was analysed in two ways; a phase locking factor (PLF) analysis and a comparison of ERPs in response to rhythmic and arrhythmic items. The PLF provides an indication of the coherence of the phase angle of a particular frequency, in this case 1.67 Hz, across trials. The observation here was a significantly higher PLF for rhythmic over arrhythmic items. Increased PLF has been taken as evidence for entrainment of neural oscillations (e.g., Stefanics et al., 2010; Lakatos et al., 2008).However, we take this explanation with caution as it is difficult to distinguish cortical entrainment from the regular reoccurrence of evoked responses (Alexandrou et al., 2018; Haegens & Zion Golumbic, 2018; Zoefel et al., 2018; Novermbre & Iannetti, 2018). Although the definition of cortical entrainment remains debated (see Peelle & Davis, 2012; Alexandrou et al., 2018), the increased PLF provides evidence that the phase of the relevant 1.67 Hz was in greater synchrony in the rhythmic compared to the arrhythmic condition.

To gain further insight into the underlying processes during encoding, ERPs for the rhythmic and arrhythmic conditions were compared. There is evidence to suggest that, similar to the established effects observed when orienting spatial selective attention (e.g., Hillyard & Anllo-Vento 1998; Luck et al., 2000), focusing attention to a moment in time results in increased amplitude of early perceptual components (Rohenkohl & Nobre, 2011; Escoffier et al., 2015). Analysis of the ERPs time locked to the stimuli showed an effect of rhythmic structure at the N1, but only for checkerboards. Specifically, there was a larger N1 for arrhythmic compared to rhythmic checkerboards, which is the opposite pattern to what would be expected according to the DAT. The effect of temporal expectancy on the N1 has both been observed (Escoffier et al., 2015) and absent in previous research (e.g., Griffin et al., 2002; Mento, 2017), and the present study also shows mixed results. The checkerboards and objects differed in several attributes: Checkerboards were three times more likely to occur than objects, and objects required additional processing to determine whether the item depicted an animal. The visual N1 has been shown to be influenced by processes such as perceptual load (Fu et al., 2008), and the content of the stimulus; whether or not it requires discrimination (Luck et al., 2000; Vogel and Luck, 2000). Thus, it is possible that the difference in probability between the two items, or, the level of processing, may have interfered with the effects of temporal structure at the N1. However, this is speculative and with so many differences between objects and checkerboards, the cause of this observed pattern requires further investigation.

However, there was an effect of temporal structure for both object types at later stages of processing, with greater posterior positivity for rhythmic compared to arrhythmic items in the Dm time interval (400-800 ms). Effects in this time interval have been suggested to provide "…an index of neural computations at the time of encoding that are predictive of accurate recall or recognition" (Paller & Wagner, 2002, p.95). Typically, the Dm effect is the comparison of hits and misses, with larger positivity for items remembered than those forgotten, but such an analysis was not possible in this study due to the low number of misses. The Dm effect largely overlaps the P300 component (but see Friedman, 1990; and Grune et al., 1996, for a dissociation of the P3b and Dm effect), in particular the P3b, the posterior component of the P300 (Polich & Comerchero, 2003), which is sensitive to the amount of attention allocated to the stimulus (Ford et al., 1994; Grune et al., 1996) and related to subsequent memory (Polich, 2007). Moreover, the P3b has been shown to be influence by temporal expectation, with a larger P3b for temporally expected items (Griffin et al., 2002; Nobre & Rohenkohl, 2011). Interestingly, the ERP effects of temporal structure at encoding also correlated with the behavioural memory effect across participants. This association was found for both the N1 effect (checkerboards only) and the Dm effect of temporal structure (both objects and checkerboards). However, this relationship was in the opposite direction to what we would have expected. That is, larger ERP effects between rhythmic and arrhythmic items at encoding were associated with smaller behavioral effects of temporal structure at recognition. Previous studies have reported associations between the magnitude of the Dm effect (hits vs misses) during encoding with later effects of recognition (e.g., Friedman & Trott, 2000). It should be noted that the present correlations do not specifically associate direct measures of memory as we did not analyze hits vs misses, instead they represent two measures affected by temporal structure; ERPs during encoding and behavioural performance during recognition. Taken together, analysis of ERPs during stimulus presentation at encoding suggests that rhythmically presented items are processed differently than those presented arrhythmically, and that this is related to behavioural effects at recognition. The pattern of results during encoding does not clearly dissociate whether the rhythm increased temporal periods of attention affecting perceptual processing or deeper encoding of items. Future research may seek to increase task difficulty in order to elicit more misses to allow for a more detailed analysis of the effect of temporal structure on items remembered versus forgotten.

Participants in the present study were largely unaware of the temporal manipulation at encoding. It is therefore unlikely that greater recognition following rhythmic compared to arrhythmic encoding can be explained by participants adopting different strategies in the two conditions. Only three of the 24 participants reported awareness of the different onset timings, and recognition scores were similar in aware and unaware participants. A similar finding was reported by Thavabalasingam et al. (2016), in which recognition was greater following structured than unstructured presentation timings regardless of whether or not participants were aware. This may suggest an implicit mechanism underlying the beneficial effect of temporal structure on memory. In another study, van de Ven et al. (2017) reported greater memory for associate pairs when the interval between the presentations of the paired items at encoding matched the interval at test (heightened temporal expectation), and importantly participants were unaware of the timing manipulation.

To speculate on how rhythmic encoding boosts recognition, one possibility is that it creates optimal processing conditions for the successful intake and storage of new information. It may lead to the formation of stronger memory traces compared to items presented in an arrhythmic manner. Indeed, it is well established that deep encoding leads to greater subsequent memory than shallow encoding, and the memory specific components examined in this study may reflect differences in the strength of the encoded representations (e.g., Brezis et al., 2016). This fits the enhanced P3b during encoding in the Dm time interval and is also corroborated with the pattern of ERP effects in the recognition task. That is, we observed an LPC old/new effect only for rhythmically encoded items, and this has previously been linked to deep processing, whilst the FN400 effect was present in both conditions and has been shown to be unaffected by depth of processing (Rugg et al., 1998). Alternatively, it is possible that rhythmic encoding is associated with recollection-based processing, which, unlike familiarity-based processing, leads to detailed conscious memory of specific items (for discussions of the dual process theory of recognition see Jacoby, 1991; Rotello, Macmillan, & Reeder, 2004; Wixted, 2007; Yonelinas, 2002; Yonelinas & Levy, 2002). Indeed, Thavabalasingam et al. (2016) reported greater recollection associated with items studied in a structured relative to an unstructured temporal framework, with no difference in familiarity. Additionally, the LPC effect was associated with rhythmic encoding in the present study, and a number of studies have linked this to recollection and the FN400 to familiarity (e.g., Curran, 2000; Curran & Cleary, 2003; Duarte et al., 2004; Rugg & Curran 2007; Voss et al., 2010). In contrast, Kafkas and Montaldi (2018) reported that temporal expectation during encoding led to greater familiarity and lower recollection for expected over unexpected items, but because the type of processing was also manipulated at encoding (free viewing to encourage familiarity and semantic encoding to encourage recollection), it is difficult to underpin the specific effect of expectation.

Alternatively, rather than rhythmic presentation providing a benefit to encoding, it is possible that arrhythmic stimulus onset has a detrimental effect on encoding (Proctor, 1983). Temporal unpredictability may create interference between the rehearsal of the item just presented and the processing of the next item. However, the beneficial effect of temporal structure was observed in Thavabalasingam et al. (2016) under incidental encoding conditions where participants were not aware that their memory would later be tested and so rehearsal was not required.

Although average trial length was constant at 1200 ms in the rhythmic and arrhythmic conditions in the present study, it should be noted that the randomly generated interstimulus interval (ISI) timings in the latter condition meant that some trials had a longer or shorter duration than the average. All stimuli were presented for precisely 600 ms, but compared to the rhythmic condition in which all events were constant, arrhythmic trials with a long ISI would have allowed additional processing time of the preceding item, and arrhythmic trials with a short ISI would have allowed less processing time. This would have balanced out over the course of the experiment and it is unlikely that subtle differences in duration rather than the temporal manipulation explain the findings. A few key points of evidence led us to this conclusion. First, presenting items for 600 ms is ample exposure duration to support recognition, and additional processing time does not further increase performance (e.g., Berry et al., 2018; Voss & Gonsalves, 2010). Second, during encoding, the difference between rhythmic and arrhythmic stimuli was observed well before item offset; the observed difference in the Dm time interval was present from around 400 ms, suggesting that temporal structure affected item specific encoding at the point at which the item was on the screen. Finally, Thavabalasingam et al. (2016) concluded based on item analyses that recognition was not mediated by differences in the length of the ISI that followed each item.

To conclude, this study highlights that rhythmic encoding leads to greater subsequent recognition than arrhythmic encoding and is associated with distinct neural processes. An FN400 old/new effect was present for both rhythmic and arrhythmically encoded items, but the LPC old/new effect was present only for rhythmically encoded items. Analysis of items presented rhythmically versus arrhythmically during encoding suggests that rhythmic structure was associated with heightened temporal expectancy, leading to greater processing relative to the arrhythmic condition.

Author Contributions

*The authors contributed equally and share first authorship.

Both authors developed the concept and design. E.V. Ward developed the experimental programme. Data collection was performed by A. Isac (see acknowledgements) under the supervision of E.V. Ward and A. Jones. E.V. Ward performed the behavioural analyses and A. Jones performed the EEG analyses. Both authors contributed towards drafting the manuscript and approved the final version for submission.

Open practice statement

De-identified data for this study along with a code-book and the data presentation scripts are posted at [https://osf.io/hv4j8/].

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