

# Brain oscillations track the formation of episodic memories in the real world

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1           **Brain oscillations track the formation of episodic**  
2                           **memories in the real world**

3  
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## 17 **Abstract**

18 Despite the well-known influence of environmental context on episodic memory, little has been  
19 done to increase contextual richness within the lab. This leaves a blind spot lingering over the  
20 neuronal correlates of episodic memory formation in day-to-day life. To address this, we presented  
21 participants with a series of words to memorise along a pre-designated route across campus while a  
22 mobile EEG system acquired ongoing neural activity. Replicating lab-based subsequent memory  
23 effects (SMEs), we identified significant low to mid frequency power decreases (<30Hz), including  
24 beta power decreases over the left inferior frontal gyrus. When investigating the oscillatory  
25 correlates of temporal and spatial context binding, we found that items strongly bound to spatial  
26 context exhibited significantly greater theta power decreases than items strongly bound to temporal  
27 context. These findings expand upon lab-based studies by demonstrating the influence of real world  
28 contextual factors that underpin memory formation.

29 *Keywords: episodic memory; context; oscillations; mobile electroencephalography*

## 30 **Introduction**

31 Episodic memory refers to rich memories of personally experienced events. The details of these  
32 memories not only encompass the event itself but also the surrounding environmental setting, such  
33 as where and when the event occurred. Environmental context change can have a profound effect  
34 on episodic memory (Godden and Baddeley, 1975; Smith and Vela, 2001). Yet despite such context  
35 change being typical in day-to-day life, these changes are rarely incorporated in neuroscientific  
36 experiments examining episodic memory (often due to the need to conduct these experiments in  
37 magnetic resonance imaging [MRI] or magnetoencephalogram [MEG] suites). In these experiments, it  
38 is possible that mechanisms relating to the encoding of environmental context are suppressed, as  
39 context remains largely consistent and therefore irrelevant to the task. This means that the neural  
40 correlates of episodic memory observed in the lab may provide an incomplete picture of episodic  
41 memory in the real world. While it is impossible to implement MEG or MRI in daily-life settings,  
42 progress has been made in the use of portable EEG outdoors (De Vos et al., 2014; Debener et al.,  
43 2012). Embracing these advances, we aimed to investigate the influence of vibrant real world  
44 environments on the electrophysiological correlates of episodic memory formation.

45 One of the most common approaches to studying episodic memory formation is the subsequent  
46 memory effect (SME). SMEs are the neural signature of successful memory formation, calculated by  
47 contrasting the neural activity at encoding which predicts later remembering with the activity that  
48 predicts later forgetting, hence isolating the activity unique to memory formation. Oscillatory SMEs  
49 are in part characterised by alpha and beta (8-12Hz; 13-30Hz) power decreases (Burke et al., 2015a;  
50 Fellner et al., 2013; Greenberg et al., 2015; Guderian et al., 2009; Hanslmayr et al., 2009;

51 Meeuwissen et al., 2011; Noh et al., 2014; Weiss and Rappelsberger, 2000). Additionally, theta has  
52 often been implicated in memory formation, although discrepancies exist in the literature with both  
53 theta power increases and decreases purported to underlie successful memory formation (Burke et  
54 al., 2015a, 2013; Fell et al., 2011; Guderian et al., 2009; Merkow et al., 2014; Noh et al., 2014; Nyhus  
55 and Curran, 2010; Staudigl and Hanslmayr, 2013). Nevertheless, beta power (13-20Hz) decreases  
56 have been shown to reliably arise over task-relevant sensory regions during successful memory  
57 formation, a result attributed to information processing (Hanslmayr et al., 2012). Critically, a recent  
58 EEG-repetitive transcranial magnetic stimulation (rTMS) study has demonstrated that beta power  
59 decreases are causally relevant to this process (Hanslmayr et al., 2014). The predictability of these  
60 beta power decreases provide a reliable benchmark to contrast with real world recordings in order  
61 to identify whether the typical lab-based SME is observable in a real world environment.

62 Beyond the validation of previous lab-based findings, portable EEG technology allows the  
63 investigation of aspects of episodic memory that only occur in their entirety in the real world, such  
64 as item-to-context binding. Item-to-context binding can be assessed via contextual clustering - a  
65 behavioural phenomenon in which several events are recalled together based on contextual  
66 similarities they share. Contextual clustering has often been demonstrated for events which share a  
67 similar temporal context (i.e. events that occurred at similar points in time; Howard & Kahana,  
68 2002). However, contextual clustering is not solely restricted to the time domain (e.g. Long, Danoff,  
69 & Kahana, 2015; Polyn, Norman, & Kahana, 2009). Of particular relevance here, studies have also  
70 demonstrated spatial contextual clustering where events that occurred in similar locations are  
71 recalled together (Copara et al., 2014; Miller, Lazarus, Polyn, & Kahana, 2013). To date, this  
72 phenomenon is predominantly studied in virtual reality where participants navigate low-resolution  
73 environments with limited visuospatial information. Vestibular and locomotion cues are distinctly  
74 lacking in many virtual reality experiments, yet lesion studies in rats have shown that these cues have  
75 been shown to have a profound impact on spatial navigation (Stackman and Herbert, 2002; Wallace  
76 et al., 2002). The absence of such cues may impede the development of a comprehensive spatial  
77 contextual representation.

78 It is also worth noting that a number of studies investigating spatial context have relied on random  
79 travel patterns to dissociate spatial and temporal contextual effects. A large number of random  
80 trajectories would inevitably mean that spatial and temporal context incidentally coincide at various  
81 points during the experiment, introducing a confounding variable and potentially trivial explanation of  
82 spatial clustering. In our experiment, we aimed to overcome this issue by using novel navigational  
83 paths that allow the observation of the independent contributions of temporal and spatial context to  
84 episodic memory formation.

85 On an oscillatory level, Long and Kahana (2015) demonstrated that temporal clustering correlates  
86 with gamma power increases in the left inferior frontal gyrus and the hippocampus during encoding.  
87 However, to the best of our knowledge, no other experiment has further investigated the  
88 relationship between neural oscillations at encoding and contextual clustering. Therefore, it remains  
89 unknown whether these patterns of activation are unique to subsequent temporal clustering or a  
90 part of a more general associative mechanism. If the former is true, then the oscillatory correlates of  
91 item-to-spatial context binding also remain unknown. *A priori* assumptions follow that subsequent  
92 temporal and spatial clustering would encompass the medial temporal lobe (MTL) – the home of  
93 place and time cells (Eichenbaum, 2014; MacDonald et al., 2011; O’Keefe, 1976). Given the intimate  
94 relationship between place cells and theta band activity, it may also be plausible to suggest that the  
95 spatial clustering effect would be observable within the theta frequency (Burgess and O’Keefe, 2011;  
96 O’Keefe and Recce, 1993).

97 It is of course important to identify potential oscillatory confounds that may arise in ‘real world’  
98 paradigms that are not present in lab-based experiments. Numerous mobile brain body imaging  
99 (MoBI; Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009) studies have demonstrated that both  
100 event-related potentials (ERPs) and oscillatory activity can be observed in moving participants (De  
101 Sanctis et al., 2014; Gramann et al., 2010; Gwin et al., 2010; Malcolm et al., 2015; Wagner et al.,  
102 2014). However, in relation to oscillatory activity, movement-related changes in power changes  
103 across the frequency spectrum (~1Hz to 90Hz). More specifically, in comparison to standing, walking  
104 can produce alpha/beta band power suppression and gamma power increases in sensorimotor areas  
105 (Castermans et al., 2014; Seeber et al., 2015, 2014; Wagner et al., 2016, 2012), whilst a loss of  
106 balance has been linked to an increase in theta band activity (Sipp et al., 2013). Importantly, these  
107 latter findings share spectral similarities with the SME. Therefore, in order to avoid potential  
108 contamination of these effects, the EEG data obtained in this experiment was acquired solely while  
109 participants were stationary.

110 In this experiment, we asked two questions; 1) can oscillatory lab-based episodic memory  
111 studies be validated in real-life settings? and 2) what are the neural correlates of temporal and spatial  
112 contextual clustering? Following a predefined route and led by the experimenter (see figure 1a and  
113 1b), participants were presented with words to encode and associate with their current location  
114 (see figure 1c), a situation similar to remembering several text messages on the way to the  
115 supermarket. Participants were shown 4 lists of 20 words, where each list was presented on a  
116 spiralling route (see figure 1a). These spiralling routes were used to help disentangle the relationship  
117 between temporal and spatial context (see methods for details). After being shown a list of words,  
118 participants were removed from the environment and completed a free recall test. Finally,  
119 participants guided the experimenter to where they thought each recalled word was shown and the

120 location was marked by GPS. We aimed to replicate the well-documented low to mid frequency  
121 power decreases (<30 Hz) in lab-based subsequent memory studies (e.g. Burke et al., 2015b;  
122 Hanslmayr and Staudigl, 2014), in particular the beta power decreases over the left inferior frontal  
123 gyrus elicited by verbal SME paradigms (Hanslmayr et al., 2011). Furthermore, we aimed to identify  
124 and dissociate the neural correlates of spatial and temporal contextual encoding. To this end, we  
125 contrasted neural activity associated with subsequent temporal clustering with that of subsequent  
126 spatial clustering. In short, this is the first experiment directly observing the neural correlates of  
127 episodic memory encoding in the real world, allowing both the validation of a large body of the  
128 episodic memory literature and the identification of how real world context affects the neural  
129 correlates of encoding.

## 130 **Materials and Methods**

### 131 *Participants*

132 29 University of Birmingham students (18-39 years, 69% female) were recruited through a  
133 participant pool and rewarded with financial compensation for participation. Nine participants were  
134 excluded from the sample due to issues in recording leading to insufficient trials (n=4), poor weather  
135 conditions leading to insufficient trials (n=2) or extreme performance in the task (recalled <15 items,  
136 or forgot <15 items across all blocks; n=3). Recording complications meant that one block was lost  
137 for 3 participants leaving only 60 trials prior to preprocessing, however as there were still a  
138 sufficient number of trials ( $\geq 15$  remembered and  $\geq 15$  forgotten) after artefact rejection these  
139 participants remained in the sample. All participants were native English speakers or had lived in an  
140 English speaking country for the past 5 years. Participants reported normal or corrected-to-normal  
141 vision. Our sample size boundary (n=20) matched similar studies which have produced reliable  
142 oscillatory subsequent memory effects (e.g. Hanslmayr, Spitzer, & Bauml, 2009). A power analysis on  
143 pilot behavioural data indicated that a sample size of 16 participants was adequate for detecting a  
144 significant behavioural effect ( $\alpha=0.05$ ;  $1-\beta=0.80$ ). Ethical approval was granted by the University of  
145 Birmingham Research Ethics Committee, complying with the Declaration of Helsinki.

### 146 *Materials*

147 80 unique abstract nouns and 80 unique locations were split into 4 blocks (20 words and locations  
148 per block). The nouns were selected from the MRC Psycholinguistic Database based on scores of  
149 low imaginability and concreteness (Coltheart, 1981). All locations within a block were found in the  
150 same large, open space on the university campus. Lists and locations were counterbalanced across  
151 participants. Words were presented in black on a light grey background using the OpenSesame  
152 experiment builder (2.9.4; Mathôt, Schreij, & Theeuwes, 2012) on a Google Nexus 7 (2013; Google,  
153 Mountain View, California) tablet running Android OS (5.1.1). Tones were elicited by the tablet and

154 passed onto a StimTracker (Cedrus Corporation, San Pedro, California), which in turn passed a  
155 trigger to the EEG amplifier. Within each block, the navigated route formed a spiral (although  
156 participants were unaware of this; see figure 1a). In figure 1a, the dotted red line depicts the  
157 temporal sequence in which each black dot (representing a presentation location) was visited. The  
158 distance between each of these black dots when following the temporal sequence was approximately  
159 20m. In contrast, the distance between the black dots on neighbouring loops was approximately 10-  
160 15m. Therefore, the black dots on neighbouring loops were closer in Euclidean distance than items  
161 presented on the same loop. To exhibit large amounts of temporal clustering, participants would  
162 have to recall items on the same loop (i.e. closer in time, further in space). Conversely, to exhibit  
163 large amounts of spatial clustering, participants would have to recall items on neighbouring loops  
164 together (i.e. closer in space, further in time). This distinction helped to disentangle the effects of  
165 temporal and spatial context while keeping rehearsal time between items constant. A Garmin eTrex  
166 30 Outdoor Handheld GPS Unit (Garmin Ltd., Canton of Schaffhausen, Switzerland) was used to  
167 navigate the route and to mark co-ordinates during the spatial memory test. The GPS could  
168 accurately pinpoint a current location to approximately within 3 metres.

#### 169 *Procedure*

170 Prior to commencing the experiment, participants were informed of the experimental procedure,  
171 completed a screening questionnaire and provided informed consent. During the encoding stage of  
172 each block, the experimenter walked the participant along a spiral path and at predefined locations  
173 stopped the participant to present them with a word on the tablet screen. When they were brought  
174 to a stop, participants were asked to immediately fixate upon the tablet screen. Critically, the  
175 participant was stationary whenever a stimulus was shown, attenuating movement-related EEG  
176 artifacts that could contaminate recordings. During stimulus presentation, the experimenter stood to  
177 the left and to the front of the participant to ensure the participant could clearly see the tablet  
178 without moving their head. After haptic input from the experimenter (given once the participant was  
179 stationary), a fixation cross was displayed in the centre of the screen for 2.5 to 3 seconds (uniformly  
180 random), followed by a target word presented for 3 seconds. The lengthy pre-stimulus interval  
181 ensured that any motor/motor-rebound effects would not contaminate EEG recordings during the  
182 presentation window. The participant then encoded the word and the location. We intentionally  
183 asked participants to encode location in order to demonstrate that participants could accurately  
184 recall spatial information. If, on a whole, participants were found to be unable to recall spatial  
185 information accurately, it would be dubious to suggest that such information could influence recall in  
186 such a way as to produce spatial contextual clustering. Participants' retention of spatial information  
187 did not influence spatial clustering (see results). After 20 locations had been visited, the participant  
188 completed a short subtraction distractor task ("starting at x, count down in steps of y, all the way to

189 zero”) to disrupt any working memory effects. The participant was then walked to a testing cubicle  
190 and given 3 minutes to freely recall as many of the words presented as possible. Subsequently, the  
191 experimenter walked the participant back outside and, using the list of recalled words as a cue, the  
192 participant attempted to return to where each word was presented. GPS co-ordinates for each of  
193 these recalled locations were recorded. After the participant had recalled as many of the locations as  
194 they could remember, the experimenter walked them to the next area in order to start the  
195 following block.

#### 196 *Behavioural Analysis*

197 Spatial accuracy of recalled locations was determined by calculating the distance between the  
198 presentation and recalled locations of each word using the Haversine formula (which corrects for  
199 the curvature of the earth), providing a parametric measure of accuracy in metres. To assess spatial  
200 and temporal clustering, we used a variation on previous methods (Kahana, 1996) to assess the  
201 extent to which a recalled item was influenced by the previously recalled items. This variation allows  
202 the direct comparison of temporal and spatial clustering, expanding upon earlier studies which have  
203 used separate methods to analyse temporal and spatial clusters (Miller, Lazarus, et al., 2013). An  
204 error term was used to identify whether participants recalled in spatial and/or temporal clusters.  
205 ‘Contextual error’ describes the extent to which an individual deviated from the immediate context  
206 when recalling events; the smaller the contextual error, the less they deviated from the immediate  
207 context and therefore the greater the contextual clustering. Contextual error was derived using the  
208 equation below:

$$209 \text{ Contextual Error} = (|(\text{Observed } Lag_{n,n-1}) - \text{Expected } Lag_{n,n-1})| + (|(\text{Observed } Lag_{n,n-2}) - \text{Expected } Lag_{n,n-2})|) / 2$$

210 Here,  $n$  refers to the recalled item under observation,  $n-1$  to the item recalled immediately before  $n$ ,  
211 and  $n-2$  to the item recalled immediately before  $n-1$ . *Observed*  $Lag_{n,n-1}$  refers to the contextual  
212 distance between the items  $n$  and  $n-1$  at encoding. Spatial contextual distance was measured in  
213 metres, while temporal distance was measured by serial lag. As each item within a block was  
214 presented approximately 25 seconds after its prior, serial lag and temporal lag are viewed as  
215 synonymous. *Expected*  $Lag_{n,n-1}$  refers to the distance between item  $n$  and the most proximal item to  $n$   
216 during encoding. *Expected*  $Lag_{n,n-2}$  refers to the distance between item  $n$  and the second most  
217 proximal item to  $n$  during encoding. Subtracting the expected lag from the observed lag provides a  
218 ‘raw’ contextual error score ranging from zero upwards, where zero indicates perfect contextual  
219 clustering during recall and any value greater than zero indicates imperfect clustering during recall.  
220 To contrast the two modalities of context, raw contextual error scores were z-transformed using  
221 the means and standard deviations of noise data. Noise data were generated by taking the observed  
222 hits, randomly assigning a recall position to them, and then calculating the contextual error. This



223 provides a 'z-transformed' contextual error score where zero indicates contextual clustering  
224 observed due to chance, and any value less than zero indicating contextual clustering greater than  
225 chance. To provide a measure of clustering rather than idiosyncratic jumps between individual items,  
226 an average lag was calculated using the two previously recalled items. This method is not expected  
227 to fundamentally change the results of previous lab-based studies; Lohnas & Kahana (2014) have  
228 demonstrated that temporal clustering in free recall is influenced by multiple recent recall items, not  
229 only the immediately preceding item. One-sample t-tests were used to examine whether participants  
230 recalled in clusters more greatly than expected by chance. A dependent-samples t-test then  
231 compared temporal and spatial contextual error scores.

### 232 *EEG Acquisition, Pre-processing and Time-Frequency Decomposition*

233 EEG was recorded using a portable 'EEGo Sports' EEG system (ANT Neuro, Enschede,  
234 Netherlands) with 65 Ag/AgCl electrodes arranged in a 10/10 system layout (including left and right  
235 mastoids, CPz as reference and AFz as ground). Impedances were kept below 20 k $\Omega$ , and the  
236 sampling rate was set to 500Hz. To facilitate source analysis, head coordinates of all electrodes and  
237 the nasion, left pre-auricular area and right pre-auricular area of each participant were taken using a  
238 Polhemus Fasttrack system (Polhemus, Colchester, VT) before commencing the experiment.

239 The data was pre-processed using the FieldTrip toolbox (Oostenveld et al., 2011). The continuous  
240 data were epoched into single trials beginning 2000ms before word presentation and ending 3000ms  
241 after word presentation. During this time window, the participant was stationary with their eyes  
242 fixated upon the tablet screen. The data was first high-passed filtered (1Hz; Butterworth IIR) and  
243 then eye-blinks, saccades and any other consistent muscular artefacts were removed using  
244 independent component analysis. Subsequently, residual irregular artefacts were removed by  
245 rejecting the corresponding trials; mean number of trials rejected = 15.45; mean number of hits  
246 remaining = 35.25 (max: 51, min. 22); mean number of misses remaining; 26.30 (max. = 42; min. =  
247 16). Artefact rejection was blind (i.e. the experimenter had no clue as to which trials belonged to  
248 which condition), yet peculiarly this led to a larger number of misses being rejected than hits.  
249 Speculatively, this may be a result of distraction; participants may have moved in response to one of  
250 the many numerous distractors in real world environments (e.g. unexpected loud noises). These  
251 physical movements would produce large artefacts in the EEG (much greater than the underlying  
252 brain signals) that must be rejected. Critically, such movement would also prevent the participant  
253 from attending to the word, leading to poorer memory performance for these trials. The mean  
254 number of trials rejected and included sum to 77 because 3 participants only had 60 trials worth of  
255 data at artefact rejection, making the mean number of trials completed 77 prior to artefact rejection.  
256 Bad channels were interpolated based on the data of neighbouring electrodes and the data was given  
257 an average reference (mean interpolated = 0.6; max. = 5; min. = 0).

258 Several previous studies indicate that electrophysiological data obtained from mobile participants is  
259 subject to more noise than their lab-based equivalents. (Castermans et al., 2014; Gwin et al., 2010;  
260 Kline et al., 2015; Snyder et al., 2015; Wagner et al., 2012). To provide an indication of the  
261 cleanliness of the data obtained here, the P300 component elicited by stimulus onset can be seen in  
262 figure 2a. The P300 component was obtained by using ICA to remove non-brain related components  
263 from the raw data and then applying a low-pass filter (15Hz). Each trial was corrected using a pre-  
264 stimulus baseline window ranging from -200ms to 0ms, Further examples of 'real world' ERPs have  
265 been demonstrated by De Vos et al. (2014) and Debener et al. (2012). In addition, a topography of  
266 this ERP is presented in figure 2b, and a time frequency representation of the data averaged over all  
267 trials time-locked to stimulus onset is presented in figure 2c.

268 Time-frequency analysis was conducted on the pre-processed dataset for each participant using 7  
269 cycle Morlet wavelets for frequencies of 3 to 30Hz in 1Hz steps; the time window was too short to  
270 effectively signals below 3Hz. Time was epoched from -1 to 2 seconds, where 0 seconds represents  
271 stimulus onset. Power was calculated at 50ms intervals within this window. For each frequency-  
272 channel pair, the data were z-transformed by first obtaining the average power over time for each  
273 trial, and then calculating the average and standard deviation of this time-averaged power across  
274 trials. This twice-averaged power was then subtracted from the observed power at each channel-  
275 frequency pair, and the output was divided by the standard deviation of the time-averaged power.  
276 Gaussian smoothing (2Hz, 200ms kernel) was then applied to the time-frequency representation to  
277 help reduce the impact of inter-individual differences in oscillatory response across time and  
278 frequencies.

### 279 *Subsequent Memory Analysis*

280 Trials were split into two categories; items where both word and location were later remembered  
281 (hits) and items where the word was later forgotten (misses). Note that as spatial memory was only  
282 test for words that were remembered, there was no location-remembered, word-forgotten  
283 condition. The data was first restricted to 0-1000ms post-stimulus between 15 and 20Hz to replicate  
284 previous beta power decreases seen in subsequent memory paradigms (for review, see Hanslmayr et  
285 al., 2012). Hits and misses for this time-frequency window were contrasted using a dependent  
286 samples t-test. A Monte-Carlo randomisation procedure using 2000 permutations was employed to  
287 correct for multiple comparisons (see Maris & Oostenveld, 2007). The clusters used in this  
288 randomisation procedure were defined by summing the t-values of individual channel-frequency-time  
289 triplets that exceeded threshold ( $\alpha = 0.05$ ).

290 Subsequently, further power changes in the time-frequency representation were examined.  
291 Following previous literature, alpha and beta power decreases were tested, while undirected theta

292 power differences were tested. Accordingly, alpha and beta tests were one-tailed, while theta power  
293 tests were two-tailed. As the non-parametric cluster analysis technique only informs us as to  
294 whether there is a significant effect between conditions within the window of interest, we used a  
295 sliding window analysis (Staudigl and Hanslmayr, 2013) to enhance the temporal and spectral  
296 specificity of our overarching SME. The sliding window (200ms by 1Hz in size, 75% overlap) was  
297 passed over the time-frequency window (-1000 to 2000ms), contrasting power differences between  
298 hits and misses within the window. In this technique, the Monte-Carlo randomisation procedure  
299 alone is not sufficient to control for multiple comparisons so the p-values for each sliding window  
300 were pooled together and thresholded using false discovery rate (FDR; Benjamini & Hochberg,  
301 1995).

### 302 *Subsequent Clustering Analysis*

303 To assess the oscillatory correlates of temporal and spatial clustering during encoding, contextual  
304 error scores were correlated with the time-frequency power spectrum. For each participant and for  
305 each time-frequency-channel point, the contextual error score for each trial was correlated with the  
306 observed power for that trial using a Spearman's Rank procedure. As less contextual error denotes  
307 greater contextual clustering, a negative r-value would indicate a power increase accompanying  
308 greater contextual clustering. To aid comprehension, each returned r-value underwent a switching  
309 of sign (+0.5 became -0.5; -0.5 became +0.5), meaning a positive r-value indicated a power increase  
310 with greater contextual clustering. The time-frequency representation of r-values was tested against  
311 the null hypothesis that there would be no correlation between power and contextual clustering.  
312 This null hypothesis was realised by creating a 'null data structure' with the same dimensions as the  
313 observed data, but with all observed data points substituted with zeros (i.e. no correlation). The  
314 observed data was then contrasted with the 'null data' in the same manner as the sliding window  
315 approach described above.

### 316 *Source Analysis*

317 Observed effects on sensor level were reconstructed in source space using individual head models in  
318 combination with the standard MRI and boundary element model (BEM) provided in the FieldTrip  
319 toolbox. The Linearly Constrained Minimum Variance (LCMV) beamformer was used to localise  
320 sources of significant activity (van Veen et al., 1997). Pre-processed data was time-locked and then  
321 shifted to source space. This placed the time-locked data onto virtual electrodes, which then  
322 underwent an identical analytical procedure to its sensor-level counterparts. P-values are presented  
323 with each source reconstruction for completeness, but as the time-frequency windows were  
324 selected because they exceeded the significance threshold on sensor level, caution should be taken  
325 when interpreting source-level p-values. These p-values were derived from a cluster-based

326 permutation (Maris & Oostenveld, 2007) across the whole window of interest, as defined by sensor-  
327 level analysis. Peak differences in activity were first deduced by sliding a spherical searchlight with a  
328 6mm radius over all voxels within the interpolated significant cluster (interpolated grid size:  
329 181x217x181mm). All voxels that fell within the sphere were summed, and the group of voxels with  
330 the largest absolute value was selected as the region of peak difference. As this approach cannot  
331 effectively handle sparse regions of activity, a follow-up visual inspection was conducted. For visual  
332 inspection, only the 1% of voxels with the most extreme t-values was examined. The results of visual  
333 inspection are only reported when they produced notable differences to the peak sphere approach.

#### 334 *Additional Analyses*

335 Several further analyses were conducted but were subject to a number of analytical issues. For  
336 transparency, these analyses are listed here, but to avoid misinterpretation of the outcomes of these  
337 analyses by those glancing over the paper, these results are not reported in the results section.  
338 Theta phase to gamma amplitude coupling was investigated using the method described by Jiang,  
339 Bahramisharif, van Gerven, and Jensen (2015) in an attempt to find similar cross-frequency coupling  
340 contextual effects to those reported by Staudigl & Hanslmayr (2013). However, no differences were  
341 found, possibly due to the overly noisy gamma activity. Furthermore, differences in source-level  
342 connectivity between the medial temporal lobe and the prefrontal cortex for high versus low  
343 contextually clustered items was investigated to test the hypothesised neural context model put  
344 forward by Polyn & Kahana (2008). Unfortunately, the difference in phase angles between virtual  
345 electrode connections were almost solely clustered around 0 and  $\pi$ , preventing any meaningful  
346 connectivity analysis (Cohen, 2015).

## 347 **Results**

### 348 *Behavioural Results*

349 On average, participants recalled 50.45% of each 20 word list and when attempting to locate  
350 where each word was presented, were on average 14.74 metres away from the presentation  
351 location. Eighty percent of participants showed less temporal contextual error (i.e. more temporal  
352 contextual clustering) than spatial contextual error (see figure 3). A one-sample t-test revealed  
353 significantly greater spatial clustering than expected by chance,  $t(19)=-5.728$ ,  $p<0.001$ , 95% CI [-  
354 2.155, -1.001], matching previous virtual reality results (Miller, Lazarus, et al., 2013). Furthermore,  
355 another one-sample t-test revealed significantly greater temporal clustering than expected by chance,  
356  $t(19)=-6.105$ ,  $p<0.001$ , 95% CI [-4.003, -1.959], again conforming to earlier findings (e.g. Kahana,  
357 1996). A dependent samples t-test revealed significantly greater temporal clustering than spatial  
358 clustering,  $t(19)=-3.921$ ,  $p<0.001$ , 95% CI [-2.152, -0.654]. To examine how contextual error relates  
359 to memory performance, the mean contextual error of each participant was correlated with their

360 average hit-rate and spatial accuracy. Temporal contextual error did not correlate with memory  
361 performance in the free recall task ( $r=-0.274$ ,  $p=0.242$ ) or spatial accuracy when returning to  
362 presentation locations ( $r=-0.237$ ,  $p = 0.315$ ); the same was true for spatial contextual error (free  
363 recall performance:  $r=-0.235$ ,  $p=0.319$ ; spatial accuracy:  $r=-0.282$ ,  $p=0.229$ ).

#### 364 *Subsequent Memory Analysis*

365         Given the robust nature of lower beta power decreases over relevant sensory regions during  
366 memory formation, we first aimed to replicate a key lab-based finding in verbal episodic memory  
367 studies: a lower beta power (15-20Hz) decrease over the left inferior frontal gyrus within 1 second  
368 of stimulus onset (for review, see Hanslmayr et al., 2012). Using a cluster-based permutation test to  
369 control for multiple comparisons across all sensors (see Maris & Oostenveld, 2007), a one-tailed  
370 dependent samples t-test revealed a significant power decrease for hits in comparison to misses  
371 between 0 and 1 second post stimulus ( $p=0.009$ ; see figure 4a and 4b). To identify whether this  
372 lower beta power decrease arose in the left inferior frontal gyrus, the window was then  
373 reconstructed on source level, undergoing the same analytical procedure as its sensor level  
374 counterpart. A one-tailed dependent samples t-test revealed a significant power decrease for hits in  
375 comparison to misses ( $p=0.026$ ). We determined peak activity by sliding a spherical searchlight with  
376 a radius of 6mm across the significant cluster and calculating the sum of activity within this sphere  
377 (see methods for details); these results were confirmed by visual inspection of the 1% of most  
378 extreme voxels within the major cluster. Peak differences in activity between later remembered and  
379 later forgotten items were localised to left superior and middle temporal poles, [MNI coord.  $x=-40$ ,  
380  $y=19$ ,  $z=-30$ ; ~BA 38], while visual inspection of the most extreme 1% of voxels within the significant  
381 cluster revealed a further difference between later remembered and later forgotten items in the left  
382 inferior frontal gyrus (IFG), [MNI coord.  $x=-39$ ,  $y=30$ ,  $z=-18$ ; ~BA 47], (see figure 4c). These results  
383 replicate the previous findings of lower beta power decreases over the left IFG following successful  
384 memory formation of verbal information (Hanslmayr et al., 2011, 2009).

385         Subsequently, a more comprehensive picture of the low-frequency SMEs was sought out using a  
386 sliding window analysis (see methods for details; Staudigl & Hanslmayr, 2013). Given the prevalent  
387 power decreases within the alpha and beta bands accompanying successful memory formation  
388 (Hanslmayr et al., 2012), one-tailed dependent samples t-tests were used to analyse the subsequent  
389 memory effect between 8 and 30 Hz. As some controversy surrounds theta band activity, two-tailed  
390 dependent samples t-tests were used for frequencies between 3 and 7 Hz. Analysis revealed  
391 significant, FDR corrected, p-values ( $p_{\text{corr}}<0.05$ ) across the frequency and time spectrum (see figure  
392 5). Specifically, low frequency theta (3-4Hz,  $p_{\text{corr}}<0.05$ ) power decreases for hits in comparison to  
393 misses were observed between 600ms and 1200ms post-stimulus; alpha (8-12Hz,  $p_{\text{corr}}<0.05$ ) power  
394 decreases for hits in comparison to misses were observed between 400ms and 800ms post-stimulus;

395 and beta (21-25Hz) power decreases for hits in comparison to misses were observed just before (-  
396 250ms to 0ms,  $p_{\text{corr}} < 0.05$ ) and later after stimulus onset (1000 to 1300ms,  $p_{\text{corr}} < 0.05$ ). These low  
397 frequency power decreases match many other effects reported in the literature (see Hanslmayr &  
398 Staudigl, 2014). It is worth noting that given the relatively short time window and the use of 7 cycle  
399 wavelets, any frequency below 3Hz could not be convolved. Therefore, a broadband delta/theta  
400 effect cannot be ruled out. It is also worth noting that the broadband appearance of the spectrogram  
401 is not likely due to a subsequent memory ERP, which has been shown to elicit a greater positivity  
402 following successful memory formation (e.g. Fernández et al., 1998). Rather, it may simply be due to  
403 the nature of the subsequent memory effect. For example, Burke et al., (2015b, 2014) have  
404 demonstrated broadband power decreases accompanying successful memory formation. The  
405 difference in power between subsequently remembered versus forgotten items did not correlate  
406 with spatial accuracy.

407 Significant regions of activity observed on sensor-level were then reconstructed on source  
408 level. Theta power decreases (3-4Hz, 600-1200ms,  $p=0.005$ ) peaked in the right superior occipital  
409 area, the right precuneus and the right cuneus, [MNI coord.  $x=19, y=-87, z=39$ ; ~BA 19]. Visual  
410 inspection of the theta source activity also revealed peak differences in activity within the left middle  
411 and inferior temporal gyri, [MNI coord.  $x=-52, y=-10, z=-26$ ; ~BA 20], and the right superior parietal  
412 lobe, [MNI coord.  $x=25, y=-64, z=53$ ; ~BA 7] (see figure 5c). Generally speaking, these theta power  
413 decreases occurred in regions associated the processing of with task-relevant stimuli (i.e. semantic  
414 processing, Pobric, Lambon Ralph, & Jefferies, 2009; Visser, Jefferies, & Lambon Ralph, 2010;  
415 visuospatial processing, Formisano et al., 2002; Sack et al., 2002), conforming to earlier findings  
416 (Greenberg et al., 2015). Alpha power decreases (8-12Hz, 500-800ms,  $p=0.005$ ) peaked in the right  
417 inferior frontal gyrus, the right superior and middle temporal poles and the right insula, [MNI coord.  
418  $x=40, y=19, z=-27$ ; ~BA 38]. Post-stimulus beta power decreases (21-25Hz, 1000-1300ms,  $p=0.003$ )  
419 peaked in the left inferior frontal gyrus, left superior temporal pole and gyrus, and the left rolandic  
420 operculum, [MNI coord.  $x=-58, y=8, z=0$ ; ~BA 48]. Pre-stimulus beta activity (21-25Hz, -250-200ms,  
421  $p=0.003$ ) could not be effectively localised using the spherical cluster, but visual search of the source  
422 revealed notable differences in the right superior parietal lobe and right postcentral gyrus, [MNI  
423 coord.  $x=27, -50, 58$ ; ~BA 7]. In summary, the real world SME observed here appears to match what  
424 is regularly reported in lab-based studies (e.g. Greenberg et al., 2015; Hanslmayr et al., 2009).

#### 425 *Subsequent Clustering Analysis*

426 Our subsequent clustering analysis was conducted on a time-frequency representation of r-  
427 values obtained from correlating the power for each channel-frequency-time data point of each trial  
428 by the clustering score of the same trial. As a first step, we examined whether the correlation  
429 between power and temporal/spatial clustering differed significantly from the null hypothesis (i.e. no

430 correlation;  $r = 0$ ). Concerning temporal clustering, the sensor level analysis (conducted as in  
431 *Subsequent Memory Analysis*) revealed no cluster exceeding the significance threshold. This is  
432 consistent with a previous study which also found no correlation between temporal clustering and  
433 low frequency power (Long & Kahana, 2015). Concerning spatial clustering however, a sliding  
434 window analysis revealed a cluster consisting of extended slow theta power decreases across the  
435 stimulus interval (3-4Hz; -1000-1000ms,  $p_{\text{corr}} < 0.05$ ), and a broader theta post-stimulus power  
436 decrease (3-6Hz; 400-900ms,  $p_{\text{corr}} < 0.05$ ), which predicted greater spatial clustering (see figure 6). In  
437 other words, these theta power decreases were associated with a greater likelihood of recalling  
438 items that were spatially proximate to one another. As above, these windows were reconstructed in  
439 source space. The post-stimulus theta power decreases (3-6Hz; 400-900ms,  $p_{\text{corr}} < 0.05$ ) peaked in  
440 the left calcarine sulcus, cuneus and superior occipital regions, [MNI coord.  $x=-8, y=-97, z=20$ ; ~BA  
441 17] (see figure 5B). Meanwhile, the peri-stimulus theta power decreases (3-4Hz; -1000-1000ms,  
442  $p_{\text{corr}} < 0.05$ ), peaked in left superior and medial frontal gyrus, [MNI coord.  $x=-8, y=39, z=51$ ; ~BA 8]  
443 (not pictured due to strong similarity with fig. 6c).

444 In a second step, we contrasted the  $r$ -values obtained by correlating theta power and temporal  
445 clustering with  $r$ -values obtained by correlating theta power and spatial clustering, in order to  
446 identify whether these theta power decreases were unique to the spatial clustering condition.  
447 Cluster analysis indicated that there was a small but significant difference between temporal  
448 clustering - theta power effects and spatial clustering - theta power effects ( $p_{\text{corr}} < 0.05$ ; see figure 7a).  
449  $T$ -values indicate that theta power decreases correlate more strongly with spatial clustering than  
450 with temporal clustering. When reconstructing this difference on source level (see figure 7b), the  
451 spatial-temporal clustering contrast (3-7Hz, 400-800ms,  $p=0.003$ ) appeared to peak in left frontal  
452 superior and medial gyri, [MNI coord.  $x=-5, y=40, z=57$ ; ~BA 8]. Visual inspection of the peak 1% of  
453 activity also revealed greater theta power decreases for spatial clustering from within the left medial  
454 temporal lobe, [MNI coord.  $x=-26, y=2, z=-35$ ; ~BA 36].

455 As can be seen in figure 7b, this difference in theta power between spatial and temporal  
456 clustering occurs in a region at the boundary of the forward model and therefore may be particularly  
457 susceptible to ocular and/or muscle artifacts. To address this concern, we repeated this analysis  
458 using only the electrodes on the outer rim of the cap (FPI, FPz, FP2, AF7, AF8, F7, F8, FT7, FT8, T7,  
459 T8, TP7, TP8, P7, P8, PO7, PO8, O1, Oz, O2) as these electrodes are most likely to contain the  
460 ocular/muscle artifacts. Being able to replicate the analysis based on these electrodes alone may  
461 indicate that these findings are a result of artifacts, however the absence of a significant difference  
462 would indicate that the result is dependent on electrodes closer to cortical sources. When  
463 replicating the sensor-level spatial-temporal clustering contrast, we found no significant difference

464 between the two conditions over the outer rim electrodes alone. This suggests that the difference in  
465 theta power between spatial and temporal clustering was not due to ocular/muscular artifacts.

## 466 **Discussion**

467 Here, we identified the oscillatory subsequent memory effect (SME) in a real-world environment.  
468 Moreover, we examined the influence of real world contextual factors (i.e. space) on episodic  
469 memory relative to contextual factors available within the lab (i.e. time). Participants donned a  
470 portable EEG setup and were presented with verbal stimuli on a tablet across the university campus.  
471 Each list was presented on a spiral path that disentangled temporal and spatial context. Successful  
472 memory formation was accompanied by strong beta power decreases over left frontal regions for  
473 items which were later remembered in comparison to those which were later forgotten.  
474 Furthermore, a broad theta power decrease was observed shortly after stimulus presentation for  
475 items later remembered, over regions including the left temporal pole and right posterior parietal  
476 cortex. Similarly, theta power decreases accompanied strong spatial clustering within left frontal  
477 regions and the medial temporal lobe when compared to temporal clustering.

478 Generally speaking, our findings corroborate what others have demonstrated within a lab setting.  
479 On a behavioural level, individuals demonstrate both temporal and spatial contextual clustering in an  
480 environment where spatial details are significantly richer than what is experienced within the lab  
481 (Miller, Lazarus, et al., 2013; Miller, Neufang, et al., 2013). Expanding on previous experiments, the  
482 spiralling presentation pattern used in this experiment helped attenuate temporal and spatial  
483 contextual overlap. Knowing that temporal clustering could not inform spatial clustering and vice  
484 versa, this experiment furthers the notion that temporal clustering and spatial clustering are  
485 autonomous phenomena.

486 On an electrophysiological level, we replicated the established low-frequency power decreases  
487 observed during successful memory formation (Burke et al., 2015a, 2014; Fellner et al., 2013;  
488 Greenberg et al., 2015; Guderian et al., 2009; Hanslmayr et al., 2009; Meeuwissen et al., 2011; Noh  
489 et al., 2014; Weiss and Rappelsberger, 2000). Source localisation of the beta power activity revealed  
490 decreases in the left frontal and temporal pole regions, both of which are associated with verbal and  
491 semantic processing (Pobric et al., 2009). Following the information-via-desynchronisation hypothesis  
492 (Hanslmayr et al., 2012), these beta power decreases would reflect verbal information processing  
493 necessary for successful memory formation. Although discussed in previous studies (Hanslmayr et  
494 al., 2009), given the aspects of this study relating to movement we reiterate that these power  
495 decreases are not viewed as oscillatory correlates of motor activity (Salenius and Hari, 2003). The  
496 participant was stationary before and during the presentation of each stimulus, so no motor  
497 component would be systematically present during stimulus presentation. If a component relating to



498 motor activity did arise, then it would be evenly distributed between later remembered and later  
499 forgotten items, and hence cancel out in the later remembered-later forgotten contrast. One could  
500 still argue that a participant plans their next movement after they are confident that they have  
501 successfully encoded a stimulus before the trial has ended. Such sensorimotor planning may indeed  
502 elicit a beta power decrease (e.g. Pfurtscheller and Neuper, 1997). While we cannot rule this out  
503 based on the results of this experiment alone, this does not fit the numerous lab-based studies (e.g.  
504 Hanslmayr et al., 2011; Long and Kahana, 2015) that have found the same beta power decrease over  
505 the left inferior frontal gyrus in paradigms that have no potential for subsequent sensorimotor  
506 planning following encoding. With evidence that familiar lab-based paradigms can be replicated in real  
507 world conditions, the field can move onto more adventurous paradigms that fully embrace real  
508 world environments.

509 We also observed significant theta power decreases following successful memory formation,  
510 particularly for items that demonstrated strong spatial clustering at recall. These power decreases  
511 may reflect a common process – possible selective communication within and across spatially diverse  
512 regions. Diversity in phase is optimal for communication as signals can arrive at a time of peak  
513 excitability and selectively communicate with receiving, down-stream, neural assemblies (Maris et al.,  
514 2016). There is a wealth of evidence to suggest theta is well suited for such communication needs  
515 (for review, see Colgin, 2013). Critically, the diversity in theta phase beneficial for communication  
516 would be reflected by theta power decreases in regions relevant to successful memory formation,  
517 especially in macro-scopic recording techniques such as EEG. In the context of the current  
518 experiment, observed theta power decreases in the temporal poles, posterior parietal cortex and  
519 medial temporal regions likely reflect the activation of, and communication between, areas  
520 responsible for the processing of semantics (e.g. Whitney, Kirk, O’Sullivan, Lambon Ralph, &  
521 Jefferies, 2011) and spatial location (Ciaramelli et al., 2010; Miller et al., 2014). Ultimately, these  
522 oscillatory dynamics allows the formation of coherent memory episodes. This account would also  
523 explain the absence of a similar theta power decrease for temporally clustered items. Temporal  
524 clustering might rely on a smaller network involving no communication with spatial processing  
525 regions. Consistent with this assumption, a previous study linked temporal clustering to high  
526 frequency (gamma) activity which might reflect the action of more local networks (Long and Kahana,  
527 2015).

528 Alternatively, the absence of a neural correlate to temporal clustering may also be a result of  
529 adapting encoding strategies across blocks. Hintzman (2016) argued that an ‘intelligent’ participant  
530 would favour a memory strategy that facilitates later recall, so an unsuccessful strategy in an early  
531 block may be adapted to aid performance in later blocks. Numerous memory strategies focus on  
532 memorising lists in the order they were presented (e.g. pegwords, story creation). Swapping

533 amongst these strategies may produce a similar degree of temporal clustering with dissimilar  
534 underlying neural correlates. That said, temporal clustering functions have been shown to remain  
535 consistent in the face of varying memory strategies and suggested to be a strategy-independent  
536 memory phenomenon (Healey and Kahana, 2014). Possibly, the absence of a clear neural correlate in  
537 this experiment was due to changes in memory strategy distorting the neural signal produced by  
538 'true' temporal clustering.

539 Interestingly, we found no neural correlate of later spatial accuracy. Perhaps the short delay between  
540 the participant being stopped at the presentation location and being asked to fixate upon the screen  
541 was sufficient to process and encode the surrounding environment. Therefore, the neural activity  
542 associated with greater spatial accuracy at retrieval may have occurred prior to the defined time  
543 window of analysis. Alternatively, participants may have only begun to process the spatial location  
544 after the stimulus had disappeared from the screen. Again, this would be outside of the period of  
545 when the EEG signal was analysed. Unfortunately, as the signal outside of the planned period was  
546 contaminated with movement-related artifacts, we were unable to explore this hypothesis.

547 Unsurprisingly, real world EEG comes with its own challenges. Here, we will take the opportunity to  
548 discuss some of these issues in hope that this will save others from experiencing the same  
549 difficulties. Firstly, our testing was highly dependent on the weather. Even the lightest of rain could  
550 affect signal quality if the scalp were to become wet (e.g. through channel bridging). Conversely,  
551 sunny and/or humid days present the same risk as participants begin to sweat more. Secondly, the  
552 equipment setup is heavy, and due to the short cables connecting the cap to the amplifier, this  
553 weight had to be carried by the participant. Undoubtedly, this will have tired participants greatly  
554 during the experiment and may have increased sweating on the scalp, again comprising EEG signal  
555 quality. In future, this weight should be distributed as greatly as possible in order to avoid participant  
556 strain, decline in cognitive performance due to fatigue and the decline in signal quality that may  
557 accompany the strain. Finally, real world experiments most likely involve complex eye-movements as  
558 participants visually explore and process the surrounding environments. Future experiments could  
559 incorporate eye-tracking to help pinpoint the onset of neural processes (e.g. scene/object  
560 processing) and identify non-brain artifacts (e.g. macro-/micro-saccades),

561 In conclusion, our findings are the first to provide strong evidence for the ecological validity of lab-  
562 based experiments investigating episodic memory formation and oscillations. More importantly, our  
563 investigation into contextual clustering highlights the importance of real world memory research.  
564 We speculate that similar virtual reality studies would not observe such strong effects of spatial  
565 contextual clustering, given the lack of vestibular and locomotion cues and low-resolution  
566 visuospatial information available in virtual reality. The real world EEG approach used here can not  
567 only pave the way towards new insights into the underpinnings of contextual details in newly formed

568 memories, but also lead to realistic investigations in other domains such as spatial navigation and  
569 beyond.

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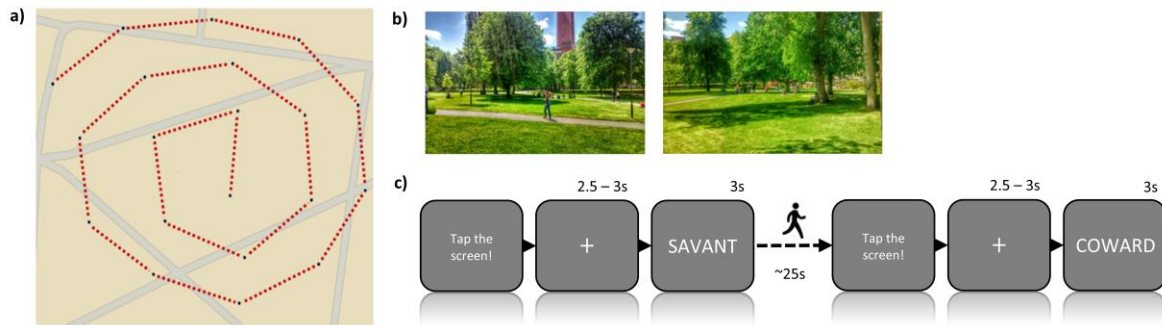
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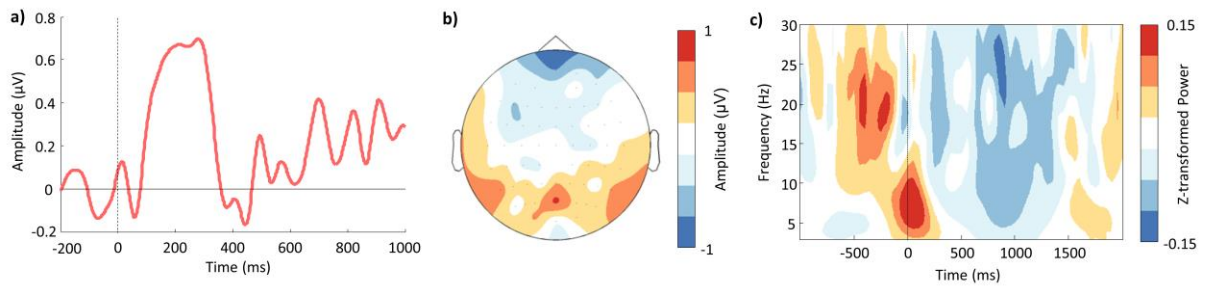
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781 Figure 1. Behavioural paradigm. a) Spiral path. Participants were guided along the red line by the experimenter. At each  
 782 black dot, the participant was shown one word to encode along with the presentation location. This route was chosen to  
 783 help attenuate contextual overlap between time and space (see methods for details). b) Example pictures of the campus  
 784 areas where the experiment took place. c) A visual representation of each trial as shown on the tablet screen. After the  
 785 experimenter tapped the screen, a word was displayed following a variable fixation window. Participants were then shown  
 786 to the next location (black dot in (a)) and the process was repeated.

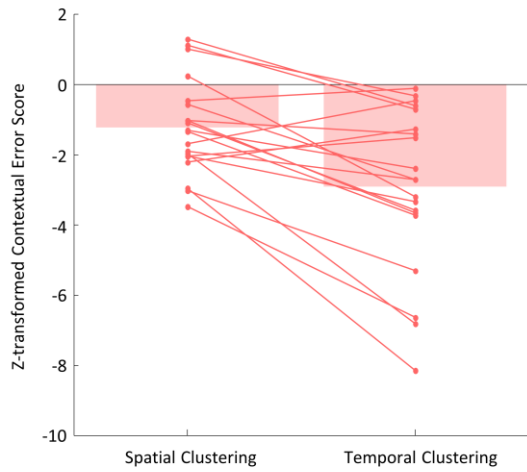
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789 Figure 2. 'Real world' EEG data. a) The P300 component elicited over parietal channels (PI, Pz, P2, PO3, POz, PO4),  
 790 averaged across all trials in response to stimulus onset. Only independent components explaining eye-blinks and  
 791 other muscular artifacts have been removed from the data. b) Topography of time-locked data, 0 to 400ms post-stimulus.  
 792 c) Time-frequency plot depicting oscillatory activity across all trials and all channels locked to stimulus onset.

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795 Figure 3. Bar plot representing the mean spatial and temporal 'z-transformed contextual error score'. Zero indicates the

796 contextual error expected by chance. A score less than zero indicates less contextual error than expected by chance, and

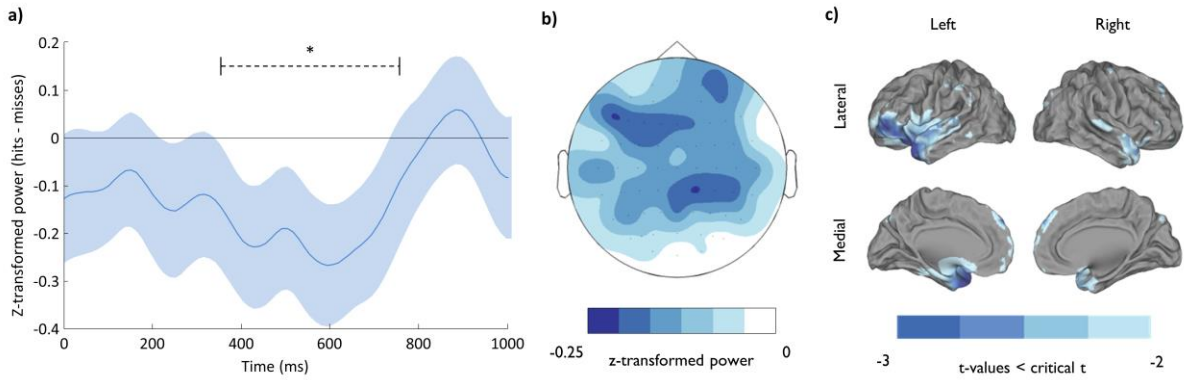
797 therefore greater contextual clustering. Individual scatter points represent the mean contextual error score of each

798 participant. Spatial and temporal clustering was significantly greater than chance ( $p < 0.001$ ). Temporal was significantly

799 greater than spatial clustering ( $p < 0.001$ ).

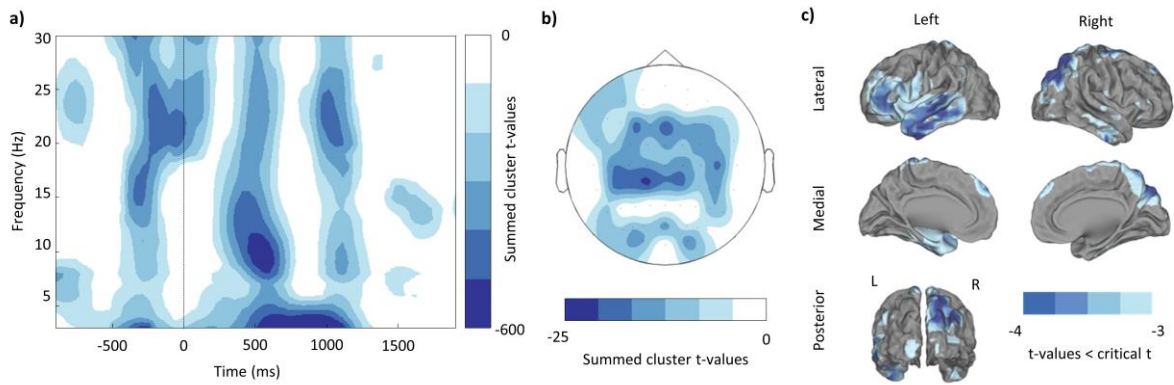
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 803 Figure 4. Subsequent memory effect (hits minus misses) in the a priori region of interest (0 to 1000ms, 15 to 20Hz, all  
 804 channels). a) The time course of z-transformed power differences between the later remembered (hits) and later forgotten  
 805 (misses) items, averaged over all channels and frequency bins with standard error of the mean. b) Topography of significant  
 806 power differences between hits and misses, averaged across the a priori time-frequency window. c) Source localisation of a  
 807 priori window of interest. Differences show a significantly greater beta power decrease in the hits condition over left  
 808 inferior frontal regions.

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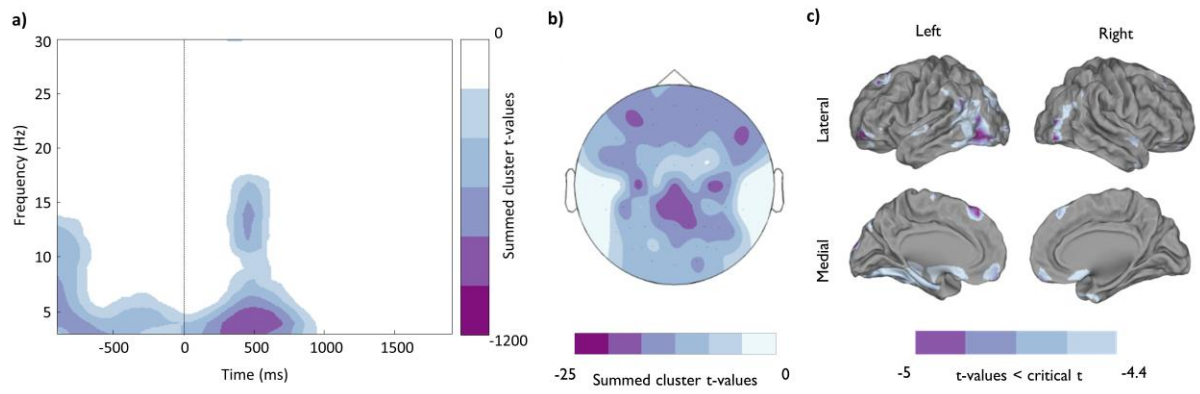
811 Figure 5. Subsequent memory effect (hits – misses) across low and mid-frequencies. a) Time-frequency representation of  
 812 cluster t-values for each significant sliding window. All non-significant FDR corrected time-frequency windows are masked.

813 b) Topography of significant difference between hits and misses for theta (3-4Hz, 600ms to 1200ms post-stimulus). c)

814 Source localisation of the significant theta effect.

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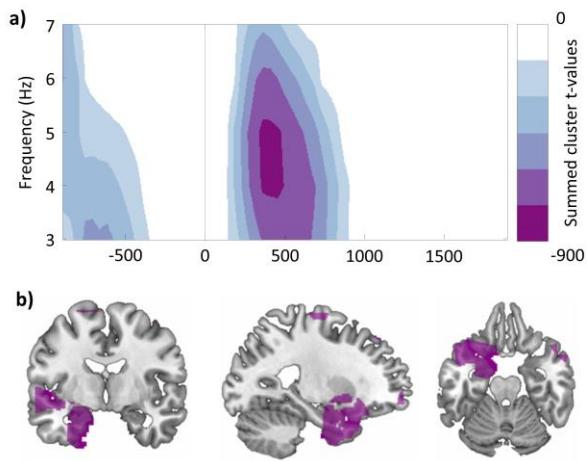


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818 Figure 6. Neural correlates of spatial clustering. a) Time-frequency representation of cluster summed t-values for windows  
 819 where the observed correlation coefficient was significantly different from the null hypothesis (i.e.  $r = 0$ ). b) Topography of  
 820 the post-stimulus theta power decrease associated with greater spatial clustering (3 – 4Hz, -1000 to 1000ms). c) Source  
 821 reconstruction of the same theta power decrease accompanying greater spatial clustering.

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825 Figure 7. Significant decreases in theta power activity for spatial clustering in comparison to temporal clustering. a) Sensor

826 level time-frequency representation of significant differences in theta power. b) Orthographic plot of source activity

827 differences between spatial clustering and temporal clustering.

828