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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
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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 correlates of temporal and spatial context binding, we found that items strongly bound to spatial 25 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

Episodic memory refers to rich memories of personally experienced events. The details of these 31 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 change being typical in day-to-day life, these changes are rarely incorporated in neuroscientific 35 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 is possible that mechanisms relating to the encoding of environmental context are supressed, as 38 39 context remains largely consistent and therefore irrelevant to the task. This means that the neural correlates of episodic memory observed in the lab may provide an incomplete picture of episodic 40 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 environments on the electrophysiological correlates of episodic memory formation. 44

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

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

Beyond the validation of previous lab-based findings, portable EEG technology allows the 62 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, & Kahana, 2015; Polyn, Norman, & Kahana, 2009). Of particular relevance here, studies have also 69 demonstrated spatial contextual clustering where events that occurred in similar locations are 70 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.

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

On an oscillatory level, Long and Kahana (2015) demonstrated that temporal clustering correlates 85 with gamma power increases in the left inferior frontal gyrus and the hippocampus during encoding. 86 However, to the best of our knowledge, no other experiment has further investigated the 87 88 relationship between neural oscillations at encoding and contextual clustering. Therefore, it remains unknown whether these patterns of activation are unique to subsequent temporal clustering or a 89 part of a more general associative mechanism. If the former is true, then the oscillatory correlates of 90 item-to-spatial context binding also remain unknown. A priori assumptions follow that subsequent 91 temporal and spatial clustering would encompass the medial temporal lobe (MTL) - the home of 92 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 across the frequency spectrum (~1Hz to 90Hz). More specifically, in comparison to standing, walking 103 104 can produce alpha/beta band power suppression and gamma power increases in sensorimotor areas (Castermans et al., 2014; Seeber et al., 2015, 2014; Wagner et al., 2016, 2012), whilst a loss of 105 106 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 contamination of these effects, the EEG data obtained is this experiment was acquired solely while 108 109 participants were stationary.

110 In this experiment, we asked two questions; I) 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 Ib), 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 spiralling route (see figure 1a). These spiralling routes were used to help disentangle the relationship 116 between temporal and spatial context (see methods for details). After being shown a list of words, 117 participants were removed from the environment and completed a free recall test. Finally, 118 participants guided the experimenter to where they thought each recalled word was shown and the 119

location was marked by GPS. We aimed to replicate the well-documented low to mid frequency 120 121 power decreases (<30 Hz) in lab-based subsequent memory studies (e.g. Burke et al., 2015b; Hanslmayr and Staudigl, 2014), in particular the beta power decreases over the left inferior frontal 122 123 gyrus elicited by verbal SME paradigms (Hanslmayr et al., 2011). Furthermore, we aimed to identify and dissociate the neural correlates of spatial and temporal contextual encoding. To this end, we 124 contrasted neural activity associated with subsequent temporal clustering with that of subsequent 125 126 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

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

146 Materials

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

passed onto a StimTracker (Cedrus Corporation, San Pedro, California), which in turn passed a 154 155 trigger to the EEG amplifier. Within each block, the navigated route formed a spiral (although participants were unaware of this; see figure 1a). In figure 1a, the dotted red line depicts the 156 157 temporal sequence in which each black dot (representing a presentation location) was visited. The distance between each of these black dots when following the temporal sequence was approximately 158 20m. In contrast, the distance between the black dots on neighbouring loops was approximately 10-159 160 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 together (i.e. closer in space, further in time). This distinction helped to disentangle the effects of 164 165 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

Prior to commencing the experiment, participants were informed of the experimental procedure, 170 completed a screening questionnaire and provided informed consent. During the encoding stage of 171 172 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 participant was stationary whenever a stimulus was shown, attenuating movement-related EEG 175 176 artifacts that could contaminate recordings. During stimulus presentation, the experiment 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 stationary), a fixation cross was displayed in the centre of the screen for 2.5 to 3 seconds (uniformly 179 180 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 information accurately, it would be dubious to suggest that such information could influence recall in 185 such a way as to produce spatial contextual clustering. Participants' retention of spatial information 186 187 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

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

196 Behavioural Analysis

Spatial accuracy of recalled locations was determined by calculating the distance between the 197 198 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 Contextual Error = ((|Observed Lag_{n,n-1}| – Expected Lag_{n,n-1}) + (|Observed Lag_{n,n-2}| – 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, and n-2 to the item recalled immediately before n-1. Observed Lag_{nn-1} refers to the contextual 211 212 distance between the items n and n-1 at encoding. Spatial contextual distance was measured in metres, while temporal distance was measured by serial lag. As each item within a block was 213 214 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 proximal item to n during encoding. Subtracting the expected lag from the observed lag provides a 217 218 '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 hits, randomly assigning a recall position to them, and then calculating the contextual error. This 222

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

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

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

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

Time-frequency analysis was conducted on the pre-processed dataset for each participant using 7 268 cycle Morlet wavelets for frequencies of 3 to 30Hz in 1hz steps; the time window was too short to 269 270 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 help reduce the impact of inter-individual differences in oscillatory response across time and 277 278 frequencies.

279 Subsequent Memory Analysis

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

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

power differences were tested. Accordingly, alpha and beta tests were one-tailed, while theta power 292 293 tests were two-tailed. As the non-parametric cluster analysis technique only informs us as to whether there is a significant effect between conditions within the window of interest, we used a 294 295 sliding window analysis (Staudigl and Hanslmayr, 2013) to enhance the temporal and spectral specificity of our overarching SME. The sliding window (200ms by 1Hz in size, 75% overlap) was 296 passed over the time-frequency window (-1000 to 2000ms), contrasting power differences between 297 hits and misses within the window. In this technique, the Monte-Carlo randomisation procedure 298 299 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, 1995). 301

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 greater contextual clustering. To aid comprehension, each returned r-value underwent a switching 308 309 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 observed data was then contrasted with the 'null data' in the same manner as the sliding window 314 315 approach described above.

316 Source Analysis

317 Observed effects on sensor level were reconstructed in source space using individual head models in combination with the standard MRI and boundary element model (BEM) provided in the FieldTrip 318 319 toolbox. The Linearly Constrained Minimum Variance (LCMV) beamformer was used to localise sources of significant activity (van Veen et al., 1997). Pre-processed data was time-locked and then 320 shifted to source space. This placed the time-locked data onto virtual electrodes, which then 321 underwent an identical analytical procedure to its sensor-level counterparts. P-values are presented 322 323 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

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

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 analyses by those glancing over the paper, these results are not reported in the results section. 337 Theta phase to gamma amplitude coupling was investigated using the method described by Jiang, 338 339 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 found, possibly due to the overly noisy gamma activity. Furthermore, differences in source-level 341 connectivity between the medial temporal lobe and the prefrontal cortex for high versus low 342 contextually clustered items was investigated to test the hypothesised neural context model put 343 344 forward by Polyn & Kahana (2008). Unfortunately, the difference in phase angles between virtual 345 electrode connections were almost solely clustered around 0 and π , 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 where each word was presented, were on average 14.74 metres away from the presentation 350 351 location. Eighty percent of participants showed less temporal contextual error (i.e. more temporal contextual clustering) than spatial contextual error (see figure 3). A one-sample t-test revealed 352 significantly greater spatial clustering than expected by chance, t(19)=-5.728, p<0.001, 95% CI [-353 2.155, -1.001], matching previous virtual reality results (Miller, Lazarus, et al., 2013). Furthermore, 354 355 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, 1996). A dependent samples t-test revealed significantly greater temporal clustering than spatial 357 clustering, t(19)=-3.921, p<0.001, 95% CI [-2.152, -0.654]. To examine how contextual error relates 358 359 to memory performance, the mean contextual error of each participant was correlated with their

average hit-rate and spatial accuracy. Temporal contextual error did not correlate with memory performance in the free recall task (r=-0.274, p=0.242) or spatial accuracy when returning to presentation locations (r=-0.237, p = 0.315); the same was true for spatial contextual error (free 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 studies: a lower beta power (15-20Hz) decrease over the left inferior frontal gyrus within I second 367 of stimulus onset (for review, see HansImayr et al., 2012). Using a cluster-based permutation test to 368 369 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 between 0 and 1 second post stimulus (p=0.009; see figure 4a and 4b). To identify whether this 371 lower beta power decrease arose in the left inferior frontal gyrus, the window was then 372 reconstructed on source level, undergoing the same analytical procedure as its sensor level 373 374 counterpart. A one-tailed dependent samples t-test revealed a significant power decrease for hits in comparison to misses (p=0.026). We determined peak activity by sliding a spherical searchlight with 375 a radius of 6mm across the significant cluster and calculating the sum of activity within this sphere 376 (see methods for details); these results were confirmed by visual inspection of the 1% of most 377 378 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 inferior frontal gyrus (IFG), [MNI coord. x=-39, y=30, z=-18; ~BA 47], (see figure 4c). These results 382 383 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 sliding window analysis (see methods for details; Staudigl & Hanslmayr, 2013). Given the prevalent 386 power decreases within the alpha and beta bands accompanying successful memory formation 387 (Hanslmayr et al., 2012), one-tailed dependent samples t-tests were used to analyse the subsequent 388 389 memory effect between 8 and 30 Hz. As some controversy surrounds theta band activity, two-tailed 390 dependent samples t-tests where used for frequencies between 3 and 7 Hz. Analysis revealed 391 significant, FDR corrected, p-values (pcorr<0.05) across the frequency and time spectrum (see figure 392 5). Specifically, low frequency theta (3-4Hz, p_{corr}<0.05) power decreases for hits in comparison to 393 misses were observed between 600ms and 1200ms post-stimulus; alpha (8-12Hz, pcorr<0.05) power 394 decreases for hits in comparison to misses were observed between 400ms and 800ms post-stimulus;

and beta (21-25Hz) power decreases for hits in comparison to misses were observed just before (-395 250ms to 0ms, p_{corr}<0.05) and later after stimulus onset (1000 to 1300ms, p_{corr}<0.05). These low 396 frequency power decreases match many other effects reported in the literature (see Hanslmayr & 397 398 Staudigl, 2014). It is worth noting that given the relatively short time window and the use of 7 cycle wavelets, any frequency below 3Hz could not be convolved. Therefore, a broadband delta/theta 399 400 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 following successful memory formation (e.g. Fernández et al., 1998). Rather, it may simply be due to 402 403 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 level. Theta power decreases (3-4Hz, 600-1200ms, p=0.005) peaked in the right superior occipital 408 409 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 decreases occurred in regions associated the processing of with task-relevant stimuli (i.e. semantic 413 processing, Pobric, Lambon Ralph, & Jefferies, 2009; Visser, Jefferies, & Lambon Ralph, 2010; 414 visuospatial processing, Formisano et al., 2002; Sack et al., 2002), conforming to earlier findings 415 (Greenberg et al., 2015). Alpha power decreases (8-12Hz, 500-800ms, p=0.005) peaked in the right 416 417 inferior frontal gyrus, the right superior and middle temporal poles and the right insula, [MNI coord. x=40, y=19, z=-27; ~BA 38]. Post-stimulus beta power decreases (21-25Hz, 1000-1300ms, p=0.003) 418 419 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 is regularly reported in lab-based studies (e.g. Greenberg et al., 2015; Hanslmayr et al., 2009). 424

425 Subsequent Clustering Analysis

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

correlation; r = 0). Concerning temporal clustering, the sensor level analysis (conducted as in 430 Subsequent Memory Analysis) revealed no cluster exceeding the significance threshold. This is 431 consistent with a previous study which also found no correlation between temporal clustering and 432 433 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_{corr} <0.05), and a broader theta post-stimulus power decrease (3-6Hz; 400-900ms, p_{corr}<0.05), which predicted greater spatial clustering (see figure 6). In 436 437 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 source space. The post-stimulus theta power decreases (3-6Hz; 400-900ms, pcorr<0.05) peaked in 439 440 the left calcarine sulcus, cuneus and superior occipital regions, [MNI coord. x=-8, y=-97, z=20; ~BA 441 [7] (see figure 5B). Meanwhile, the peri-stimulus theta power decreases (3-4Hz; -1000-1000ms, pcorr<0.05), peaked in left superior and medial frontal gyrus, [MNI coord. x=-8, y=39, z=51; ~BA 8] 442 443 (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 clustering - theta power effects and spatial clustering - theta power effects (p_{corr}<0.05; see figure 7a). 448 T-values indicate that theta power decreases correlate more strongly with spatial clustering than 449 with temporal clustering. When reconstructing this difference on source level (see figure 7b), the 450 spatial-temporal clustering contrast (3-7Hz, 400-800ms, p=0.003) appeared to peak in left frontal 451 452 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 temporal lobe, [MNI coord. x=-26, y=2, z=-35; ~BA 36]. 454

As can be seen in figure 7b, this difference in theta power between spatial and temporal 455 456 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 (FP1, 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 indicate that these findings are a result of artifacts, however the absence of a significant difference 461 would indicate that the result is dependent on electrodes closer to cortical sources. When 462 463 replicating the sensor-level spatial-temporal clustering contrast, we found no significant difference

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

466 **Discussion**

Here, we identified the oscillatory subsequent memory effect (SME) in a real-world environment. 467 468 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 memory formation was accompanied by strong beta power decreases over left frontal regions for 472 473 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 items later remembered, over regions including the left temporal pole and right posterior parietal 475 476 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 spiralling presentation pattern used in this experiment helped attenuate temporal and spatial 482 contextual overlap. Knowing that temporal clustering could not inform spatial clustering and vice 483 484 versa, this experiment furthers the notion that temporal clustering and spatial clustering are 485 autonomous phenomena.

On an electrophysiological level, we replicated the established low-frequency power decreases 486 487 observed during successful memory formation (Burke et al., 2015a, 2014; Fellner et al., 2013; Greenberg et al., 2015; Guderian et al., 2009; Hanslmayr et al., 2009; Meeuwissen et al., 2011; Noh 488 et al., 2014; Weiss and Rappelsberger, 2000). Source localisation of the beta power activity revealed 489 490 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 (HansImayr 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 decreases are not viewed as oscillatory correlates of motor activity (Salenius and Hari, 2003). The 495 496 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

motor activity did arise, then it would be evenly distributed between later remembered and later 498 forgotten items, and hence cancel out in the later remembered-later forgotten contrast. One could 499 still argue that a participant plans their next movement after they are confident that they have 500 501 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. Hanslmayr et al., 2011; Long and Kahana, 2015) that have found the same beta power decrease over 504 505 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 may reflect a common process - possible selective communication within and across spatially diverse 511 512 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 would be reflected by theta power decreases in regions relevant to successful memory formation, 516 517 especially in macro-scopic recording techniques such as EEG. In the context of the current experiment, observed theta power decreases in the temporal poles, posterior parietal cortex and 518 519 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, & Jefferies, 2011) and spatial location (Ciaramelli et al., 2010; Miller et al., 2014). Ultimately, these 521 522 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, 2015). 527

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

amongst these strategies may produce a similar degree of temporal clustering with dissimilar underlying neural correlates. That said, temporal clustering functions have been shown to remain consistent in the face of varying memory strategies and suggested to be a strategy-independent memory phenomenon (Healey and Kahana, 2014). Possibly, the absence of a clear neural correlate in this experiment was due to changes in memory strategy distorting the neural signal produced by '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 during the experiment and may have increased sweating on the scalp, again comprising EEG signal 554 555 quality. In future, this weight should be distributed as greatly as possible in order to avoid participant strain, decline in cognitive performance due to fatigue and the decline in signal quality that may 556 557 accompany the strain. Finally, real world experiments most likely involve complex eye-movements as participants visually explore and process the surrounding environments. Future experiments could 558 559 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),

In conclusion, our findings are the first to provide strong evidence for the ecological validity of labbased experiments investigating episodic memory formation and oscillations. More importantly, our investigation into contextual clustering highlights the importance of real world memory research. We speculate that similar virtual reality studies would not observe such strong effects of spatial contextual clustering, given the lack of vestibular and locomotion cues and low-resolution visuospatial information available in virtual reality. The real world EEG approach used here can not 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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574 **References**

- 575 Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: A practical and powerful 576 approach to multiple testing. J. R. Stat. Soc. Ser. B 57, 289–300.
- Burgess, N., O'Keefe, J., 2011. Models of place and grid cell firing and theta rhythmicity. Curr. Opin.
 Neurobiol. 21, 734–744. doi:10.1016/j.conb.2011.07.002
- 579 Burke, J.F., Long, N.M., Zaghloul, K.A., Sharan, A.D., Sperling, M.R., Kahana, M.J., 2014. Human
- intracranial high-frequency activity maps episodic memory formation in space and time.
 Neuroimage 85, 834–843. doi:10.1016/j.neuroimage.2013.06.067
- Burke, J.F., Merkow, M.B., Jacobs, J., Kahana, M.J., Zaghloul, K.A., 2015a. Brain computer interface to
 enhance episodic memory in human participants. Front. Hum. Neurosci. 8, 1–10.
 doi:10.3389/fnhum.2014.01055
- Burke, J.F., Ramayya, A.G., Kahana, M.J., 2015b. Human intracranial high-frequency activity during
 memory processing: Neural oscillations or stochastic volatility? Curr. Opin. Neurobiol. 31,
 104–110. doi:10.1016/j.conb.2014.09.003
- Burke, J.F., Zaghloul, K. a., Jacobs, J., Williams, R.B., Sperling, M.R., Sharan, a. D., Kahana, M.J., 2013.
 Synchronous and asynchronous theta and gamma activity during episodic memory formation. J.
 Neurosci. 33, 292–304. doi:10.1523/JNEUROSCI.2057-12.2013
- 591 Castermans, T., Duvinage, M., Cheron, G., Dutoit, T., 2014. About the cortical origin of the low592 delta and high-gamma rhythms observed in EEG signals during treadmill walking. Neurosci. Lett.
 593 561, 166–170. doi:10.1016/j.neulet.2013.12.059
- 594 Ciaramelli, E., Rosenbaum, R.S., Solcz, S., Levine, B., Moscovitch, M., 2010. Mental space travel:
- 595 Damage to posterior parietal cortex prevents egocentric navigation and reexperiencing of
- remote spatial memories. J. Exp. Psychol. Learn. Mem. Cogn. 36, 619–634.
- 597 doi:10.1037/a0019181
- Cohen, M.X., 2015. Effects of time lag and frequency matching on phase-based connectivity. J.
 Neurosci. Methods 250, 137–146. doi:10.1016/j.jneumeth.2014.09.005

- Colgin, L.L., 2013. Mechanisms and functions of theta rhythms. Annu. Rev. Neurosci. 36, 295–312.
 doi:10.1146/annurev-neuro-062012-170330
- 602 Coltheart, M., 1981. The MRC psycholinguistic database. Q. J. Exp. Psychol. 33, 497–505.
 603 doi:10.1080/14640748108400805
- 604 Copara, M.S., Hassan, A.S., Kyle, C.T., Libby, L.A., Ranganath, C., Ekstrom, A.D., 2014.
- 605 Complementary roles of human hippocampal subregions during retrieval of spatiotemporal
- 606 context. J. Neurosci. 34, 6834–6842. doi:10.1523/JNEUROSCI.5341-13.2014
- De Sanctis, P., Butler, J.S., Malcolm, B.R., Foxe, J.J., 2014. Recalibration of inhibitory control systems
 during walking-related dual-task interference: A Mobile Brain-Body Imaging (MOBI) Study.
 Neuroimage 94, 55–64. doi:10.1016/j.neuroimage.2014.03.016
- 610 De Vos, M., Gandras, K., Debener, S., 2014. Towards a truly mobile auditory brain-computer

611 interface: Exploring the P300 to take away. Int. J. Psychophysiol. 91, 46–53.

- 612 doi:10.1016/j.ijpsycho.2013.08.010
- Debener, S., Minow, F., Emkes, R., Gandras, K., de Vos, M., 2012. How about taking a low-cost,
 small, and wireless EEG for a walk? Psychophysiology 49, 1617–1621. doi:10.1111/j.14698986.2012.01471.x
- Eichenbaum, H., 2014. Time cells in the hippocampus: a new dimension for mapping memories. Nat.
 Rev. Neurosci. 15. doi:10.1038/nrn3827
- Fell, J., Ludowig, E., Staresina, B.P., Wagner, T., Kranz, T., Elger, C.E., Axmacher, N., 2011. Medial
 temporal theta/alpha power enhancement precedes successful memory encoding: Evidence
 based on intracranial EEG. J. Neurosci. 31, 5392–5397. doi:10.1523/JNEUROSCI.3668-10.2011
- Fellner, M.-C., Bäuml, K.-H.T., Hanslmayr, S., 2013. Brain oscillatory subsequent memory effects
 differ in power and long-range synchronization between semantic and survival processing.

623 Neuroimage 79, 361–370. doi:10.1016/j.neuroimage.2013.04.121

624 Fernández, G., Weyerts, H., Tendolkar, I., Smid, H.G.O.M., Scholz, M., Heinze, H.-J., 1998. Event-

625 related potentials of verbal encoding into episodic memory: Dissociation between the effects of

- 626 subsequent memory performance and distinctiveness. Psychophysiology 35, 709–720.
- 627 doi:10.1111/1469-8986.3560709
- Formisano, E., Linden, D.E., Di Salle, F., Trojano, L., Esposito, F., Sack, A.T., Grossi, D., Zanella, F.E.,
 Goebel, R., 2002. Tracking the mind's image in the brain I: time-resolved fMRI during
 visuospatial mental imagery. Neuron 35, 185–194. doi:10.1016/S0896-6273(02)00747-X
- Godden, D.R., Baddeley, A.D., 1975. Context-dependent memory in two natural environments: On
 land and underwater. Br. J. Psychol. 66, 325–331. doi:10.1111/j.2044-8295.1975.tb01468.x

- Gramann, K., Gwin, J.T., Bigdely-Shamlo, N., Ferris, D.P., Makeig, S., 2010. Visual evoked responses
 during standing and walking. Front. Hum. Neurosci. 4, 202. doi:10.3389/fnhum.2010.00202
- Greenberg, J.A., Burke, J.F., Haque, R., Kahana, M.J., Zaghloul, K.A., 2015. Decreases in theta and
 increases in high frequency activity underlie associative memory encoding. Neuroimage 114,

637 257–63. doi:10.1016/j.neuroimage.2015.03.077

Guderian, S., Schott, B.H., Richardson-Klavehn, a., Duzel, E., 2009. Medial temporal theta state

before an event predicts episodic encoding success in humans. Proc. Natl. Acad. Sci. 106, 5365–
5370. doi:10.1073/pnas.0900289106

- Gwin, J.T., Gramann, K., Makeig, S., Ferris, D.P., 2010. Removal of movement artifact from highdensity EEG recorded during walking and running. J. Neurophysiol. 103, 3526–34.
 doi:10.1152/jn.00105.2010
- Hanslmayr, S., Matuschek, J., Fellner, M.-C., 2014. Entrainment of prefrontal beta oscillations induces

an endogenous echo and impairs memory formation. Curr. Biol. 24, 904–909.

646 doi:10.1016/j.cub.2014.03.007

- Hanslmayr, S., Spitzer, B., Bauml, K.-H., 2009. Brain oscillations dissociate between semantic and
 nonsemantic encoding of episodic memories. Cereb. Cortex 19, 1631–1640.
 doi:10.1093/cercor/bhn197
- Hanslmayr, S., Staudigl, T., 2014. How brain oscillations form memories--a processing based
 perspective on oscillatory subsequent memory effects. Neuroimage 85 Pt 2, 648–655.
 doi:10.1016/j.neuroimage.2013.05.121
- Hanslmayr, S., Staudigl, T., Fellner, M.-C., 2012. Oscillatory power decreases and long-term memory:
 the information via desynchronization hypothesis. Front. Hum. Neurosci. 6, 1–12.
 doi:10.3389/fnhum.2012.00074
- Hanslmayr, S., Volberg, G., Wimber, M., Raabe, M., Greenlee, M.W., Bauml, K.-H.T., 2011. The
 relationship between brain oscillations and BOLD signal during memory formation: A combined
 EEG-fMRI study. J. Neurosci. 31, 15674–15680. doi:10.1523/JNEUROSCI.3140-11.2011
- Healey, M.K., Kahana, M.J., 2014. Is memory search governed by universal principles or idiosyncratic
 strategies? J. Exp. Psychol. Gen. 143, 575–596. doi:10.1037/a0033715
- Hintzman, D.L., 2016. Is memory organized by temporal contiguity? Mem. Cognit. 44, 365–375.
 doi:10.3758/s13421-015-0573-8
- Howard, M.W., Kahana, M.J., 2002. A distributed representation of temporal context. J. Math.
 Psychol. 46, 269–299. doi:10.1006/jmps.2001.1388
- Jiang, H., Bahramisharif, A., van Gerven, M. a. J., Jensen, O., 2015. Measuring directionality between

- 666 neuronal oscillations of different frequencies. Neuroimage 118, 359–367.
- 667 doi:10.1016/j.neuroimage.2015.05.044
- Kahana, M.J., 1996. Associative retrieval processes in free recall. Mem. Cognit. 24, 103–109.
 doi:10.3758/BF03197276
- Kline, J.E., Huang, H.J., Snyder, K.L., Ferris, D.P., 2015. Isolating gait-related movement artifacts in
 electroencephalography during human walking. J. Neural Eng. 12, 046022. doi:10.1088/17412560/12/4/046022
- Lohnas, L.J., Kahana, M.J., 2014. Compound cuing in free recall. J. Exp. Psychol. Learn. Mem. Cogn.
 40, 12–24. doi:10.1037/a0033698
- Long, N.M., Danoff, M.S., Kahana, M.J., 2015. Recall dynamics reveal the retrieval of emotional
 context. Psychon. Bull. Rev. doi:10.3758/s13423-014-0791-2
- Long, N.M., Kahana, M.J., 2015. Successful memory formation is driven by contextual encoding in the
 core memory network. Neuroimage 119, 332–337. doi:10.1016/j.neuroimage.2015.06.073
- MacDonald, C.J., Lepage, K.Q., Eden, U.T., Eichenbaum, H., 2011. Hippocampal "time cells" bridge
 the gap in memory for discontiguous events. Neuron 71, 737–749.
 doi:10.1016/j.neuron.2011.07.012
- Makeig, S., Gramann, K., Jung, T.P., Sejnowski, T.J., Poizner, H., 2009. Linking brain, mind and
 behavior. Int. J. Psychophysiol. 73, 95–100. doi:10.1016/j.ijpsycho.2008.11.008
- Malcolm, B.R., Foxe, J.J., Butler, J.S., De Sanctis, P., 2015. The aging brain shows less flexible
- reallocation of cognitive resources during dual-task walking: A mobile brain/body imaging
 (MoBI) study. Neuroimage 117, 230–42. doi:10.1016/j.neuroimage.2015.05.028
- Maris, E., Fries, P., van Ede, F., 2016. Diverse phase relations among neuronal rhythms and their
 potential function. Trends Neurosci. xx, 1–14. doi:10.1016/j.tins.2015.12.004
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci.
 Methods 164, 177–90. doi:10.1016/j.jneumeth.2007.03.024
- Mathôt, S., Schreij, D., Theeuwes, J., 2012. OpenSesame: an open-source, graphical experiment
 builder for the social sciences. Behav. Res. Methods 44, 314–324. doi:10.3758/s13428-0110168-7
- 694 Meeuwissen, E.B., Takashima, A., Fernandez, G., Jensen, O., 2011. Evidence for human Fronto-
- 695 Central gamma activity during long-term memory encoding of word sequences. PLoS One 6.
 696 doi:10.1371/journal.pone.0021356
- 697 Merkow, M.B., Burke, J.F., Stein, J.M., Kahana, M.J., 2014. Prestimulus theta in the human

- hippocampus predicts subsequent recognition but not recall. Hippocampus 24, 1562–1569.
 doi:10.1002/hipo.22335.Prestimulus
- Miller, A.M.P., Vedder, L.C., Law, L.M., Smith, D.M., 2014. Cues, context, and long-term memory: the
 role of the retrosplenial cortex in spatial cognition. Front. Hum. Neurosci. 8, 1–15.
 doi:10.3389/fnhum.2014.00586
- Miller, J.F., Lazarus, E.M., Polyn, S.M., Kahana, M.J., 2013a. Spatial clustering during memory search. J.
 Exp. Psychol. Learn. Mem. Cogn. 39, 773–781. doi:10.1037/a0029684
- Miller, J.F., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, I., Hefft, S., Merkow, M., Polyn,
 S.M., Jacobs, J., Kahana, M.J., Schulze-Bonhage, A., 2013b. Neural activity in human hippocampal
 formation reveals the spatial context of retrieved memories. Science (80-.). 342, 1111–1114.
 doi:10.1126/science.1244056
- Noh, E., Herzmann, G., Curran, T., De Sa, V.R., 2014. Using single-trial EEG to predict and analyze
- subsequent memory. Neuroimage 84, 712–723. doi:10.1016/j.neuroimage.2013.09.028
- Nyhus, E., Curran, T., 2010. Functional role of gamma and theta oscillations in episodic memory.
 Neurosci. Biobehav. Rev. 34, 1023–1035. doi:10.1016/j.neubiorev.2009.12.014
- O'Keefe, J., 1976. Place units in the hippocampus of the freely moving rat. Exp. Neurol. 51, 78–109.
 doi:10.1016/0014-4886(76)90055-8
- O'Keefe, J., Recce, M.L., 1993. Phase relationship between hippocampal place units and the EEG
 theta rhythm. Hippocampus 3, 317–330. doi:10.1002/hipo.450030307
- 717 Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: Open source software for
- advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell.
 Neurosci. 2011, 1–9. doi:10.1155/2011/156869
- Pfurtscheller, G., Neuper, C., 1997. Motor imagery activates primary sensorimotor area in humans.
 Neurosci. Lett. 239, 65–68. doi:10.1016/S0304-3940(97)00889-6
- Pobric, G., Lambon Ralph, M. a., Jefferies, E., 2009. The role of the anterior temporal lobes in the
 comprehension of concrete and abstract words: rTMS evidence. Cortex 45, 1104–1110.
 doi:10.1016/j.cortex.2009.02.006
- Polyn, S.M., Kahana, M.J., 2008. Memory search and the neural representation of context. Trends
 Cogn. Sci. 12, 24–30. doi:10.1016/j.tics.2007.10.010
- Polyn, S.M., Norman, K.A., Kahana, M.J., 2009. A context maintenance and retrieval model of
 organizational processes in free recall. Psychol. Rev. 116, 129–156. doi:10.1037/a0014420.A
- 729 Sack, A.T., Sperling, J.M., Prvulovic, D., Formisano, E., Goebel, R., Di Salle, F., Dierks, T., Linden,

- D.E.J., 2002. Tracking the mind's image in the brain II: Transcranial magnetic stimulation reveals
 parietal asymmetry in visuospatial imagery. Neuron 35, 195–204. doi:10.1016/S0896-
- 732 6273(02)00745-6
- Salenius, S., Hari, R., 2003. Synchronous cortical oscillatory activity during motor action. Curr. Opin.
 Neurobiol. 13, 678–684. doi:10.1016/j.conb.2003.10.008
- Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., M??ller-Putz, G.R., 2015. High and low gamma
 EEG oscillations in central sensorimotor areas are conversely modulated during the human gait
- 737 cycle. Neuroimage 112, 318–326. doi:10.1016/j.neuroimage.2015.03.045
- Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., Muller-Putz, G.R., 2014. EEG beta suppression
 and low gamma modulation are different elements of human upright walking. Front. Hum.
 Neurosci. 8, 1–9. doi:10.3389/fnhum.2014.00485
- 741 Sipp, A.R., Gwin, J.T., Makeig, S., Ferris, D.P., 2013. Loss of balance during balance beam walking
- elicits a multifocal theta band electrocortical response. J. Neurophysiol. 110, 2050–60.
 doi:10.1152/jn.00744.2012
- Smith, S.M., Vela, E., 2001. Environmental context-dependent memory: A review and meta-analysis.
 Psychon. Bull. Rev. 8, 203 220. doi:10.3758/BF03196157
- 746 Snyder, K.L., Kline, J.E., Huang, H.J., Ferris, D.P., 2015. Independent Component Analysis of Gait-
- Related Movement Artifact Recorded using EEG Electrodes during Treadmill Walking. Front.
 Hum. Neurosci. 9, 639. doi:10.3389/fnhum.2015.00639
- Stackman, R.W., Herbert, A.M., 2002. Rats with lesions of the vestibular system require a visual
 landmark for spatial navigation. Behav. Brain Res. 128, 27–40. doi:10.1016/S01664328(01)00270-4
- Staudigl, T., Hanslmayr, S., 2013. Theta oscillations at encoding mediate the context-dependent
 nature of human episodic memory. Curr. Biol. 23, 1101–1106.
- van Veen, B., van Drongelen, W., Yuchtman, M., Suzuki, A., 1997. Localization of brain electrical
- activity via linearly constrained minimum variance spatial filtering. IEEE Trans. Biomed. Eng. 44,
 867–880. doi:10.1109/10.623056
- Visser, M., Jefferies, E., Lambon Ralph, M., 2010. Semantic processing in the anterior temporal lobes:
 a meta-analysis of the functional neuroimaging literature. J. Cogn. Neurosci. 22, 1083–1094.
 doi:10.1162/jocn.2009.21309
- Wagner, J., Makeig, S., Gola, M., Neuper, C., Muller-Putz, G., 2016. Distinct Band Oscillatory
 Networks Subserving Motor and Cognitive Control during Gait Adaptation. J. Neurosci. 36,
 2212–2226. doi:10.1523/JNEUROSCI.3543-15.2016

Wagner, J., Solis-Escalante, T., Grieshofer, P., Neuper, C., Müller-Putz, G., Scherer, R., 2012. Level of
 participation in robotic-assisted treadmill walking modulates midline sensorimotor EEG
 rhythms in able-bodied subjects. Neuroimage 63, 1203–1211.

766 doi:10.1016/j.neuroimage.2012.08.019

- Wagner, J., Solis-Escalante, T., Scherer, R., Neuper, C., Müller-Putz, G., 2014. It's how you get there:
 walking down a virtual alley activates premotor and parietal areas. Front. Hum. Neurosci. 8, 93.
 doi:10.3389/fnhum.2014.00093
- Wallace, D.G., Hines, D.J., Pellis, S.M., Whishaw, I.Q., 2002. Vestibular information is required for
 dead reckoning in the rat. J. Neurosci. 22, 10009–10017. doi:22/22/10009 [pii]
- Weiss, S., Rappelsberger, P., 2000. Long-range EEG synchronization during word encoding correlates
 with successful memory performance. Cogn. Brain Res. 9, 299–312. doi:10.1016/S09266410(00)00011-2
- Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. a., Jefferies, E., 2011. The neural organization
 of semantic control: TMS evidence for a distributed network in left inferior frontal and
- 777 posterior middle temporal gyrus. Cereb. Cortex 21, 1066–1075. doi:10.1093/cercor/bhq180

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

to the next location (black dot in (a)) and the process was repeated.



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Figure 2. 'Real world' EEG data. a) The P300 component elicited over parietal channels (P1, Pz, P2, PO3, POz, PO4),
averaged across all trials in response to stimulus onset. Only independent components explaining eye-blinks, saccades and
other muscular artifacts have been removed from the data. b) Topography of time-locked data, 0 to 400ms post-stimulus.

c) Time-frequency plot depicting oscillatory activity across all trials and all channels locked to stimulus onset.



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Figure 3. Bar plot representing the mean spatial and temporal 'z-transformed contextual error score'. Zero indicates the contextual error expected by chance. A score less than zero indicates less contextual error than expected by chance, and therefore greater contextual clustering. Individual scatter points represent the mean contextual error score of each 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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Figure 4. Subsequent memory effect (hits minus misses) in the a priori region of interest (0 to 1000ms, 15 to 20Hz, all channels). a) The time course of z-transformed power differences between the later remembered (hits) and later forgotten (misses) items, averaged over all channels and frequency bins with standard error of the mean. b) Topography of significant power differences between hits and misses, averaged across the a priori time-frequency window. c) Source localisation of a priori window of interest. Differences show a significantly greater beta power decrease in the hits condition over left inferior frontal regions.

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

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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Figure 6. Neural correlates of spatial clustering. a) Time-frequency representation of cluster summed t-values for windows819where the observed correlation coefficient was significantly different from the null hypothesis (i.e. r = 0). b) Topography of

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.



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

level time-frequency representation of significant differences in theta power. b) Orthographic plot of source activitydifferences between spatial clustering and temporal clustering,