

Reactivation of neural patterns during memory reinstatement supports encoding specificity

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20 **Abstract**

21 Encoding specificity states that encoding and retrieving items in the same modality benefits
22 memory, compared to encoding and retrieving in different modalities. In neural terms, this can
23 be expressed as memory cues resonating with stored engrams; the more they overlap the better
24 memory performance. We used temporal pattern analysis in MEG in a sensory match/mismatch
25 memory paradigm (i.e. items presented aurally or visually) to track this resonance process. A
26 computational model predicted that reactivation of encoding-related sensory patterns has
27 opposing effects depending on the match or mismatch between memory cue and encoding
28 modality. Behavioural performance was better in the match than the mismatch condition. Neural
29 pattern reinstatement of MEG activity benefitted memory only in the match condition, but
30 impaired memory in the mismatch condition. These effects were only obtained for aurally but
31 not visually encoded words. The results suggest that reactivation of encoding-related neural
32 patterns underlies encoding specificity.

33

34

35

36 **Introduction**

37 A memory cue is more effective when it overlaps with what has been studied. For instance, we
38 are doing better in remembering when the context between encoding and retrieval is the same,
39 compared to when they differ. A classic demonstration of this effect comes from Godden and
40 Baddeley (Godden and Baddeley, 1975) who showed that the chances of retrieving a memory are

41 higher when the environmental context during retrieval is the same as the one in which the item
42 has been studied; i.e. items that are studied and retrieved on land (as opposed to when they are
43 studied under water and retrieved on land). Similar effects have been observed with
44 matching/non-matching background movies (Smith and Manzano, 2010; Staudigl, Vollmar,
45 Noachtar, & Hanslmayr, 2015), or with different encoding/retrieval operations (i.e. rhyme vs
46 semantic processing, (Morris, Bransford, & Franks, 1977). Similar effects have also been found
47 with manipulating the modality in which items are presented at encoding and retrieval, for
48 instance using pictures and words (Bauch and Otten, 2012; Mcdermott and Roediger, 1994), or
49 presenting words visually and aurally (Mulligan and Osborn, 2009). In cognitive psychology
50 these match/mismatch effects can be subsumed under the terms Encoding Specificity Principle
51 (Tulving and Thomson, 1973), or Transfer Appropriate Processing (Morris, et al., 1977). Both
52 concepts highlight a basic organizing principle of human memory: The likelihood of
53 remembering a certain memory increases with the degree to which a reminder that is provided
54 during retrieval, resonates with a stored engram of that memory, i.e. interacts with a neural
55 pattern that was established during encoding (Rugg, Johnson, Park, & Uncapher, 2008; Tulving,
56 1983).

57 Supporting evidence for a role of neural pattern reinstatement for memory retrieval comes from a
58 number of studies showing reinstatement of encoding patterns during retrieval (Jafarpour,
59 Fuentemilla, Horner, Penny, & Duzel, 2014; Johnson, McDuff, Rugg, & Norman, 2009; Kerrén,
60 Linde-Domingo, Hanslmayr, & Wimber, 2018; S. Michelmann, Bowman, & Hanslmayr, 2016;
61 Sebastian Michelmann, Bowman, & Hanslmayr, 2018; Sebastian Michelmann, Staresina,
62 Bowman, & Hanslmayr, 2018; Polyn, Natu, Cohen, & Norman, 2005; Schreiner, Doeller,
63 Jensen, Rasch, & Staudigl, 2018; Staresina, Henson, Kriegeskorte, & Alink, 2012; Staresina et

64 al., 2016; Yaffe et al., 2014). These neural patterns can be detected using various multivariate
65 analysis approaches in order to identify reactivation of neural patterns in space (Jafarpour, et al.,
66 2014; Polyn, et al., 2005; Staresina, et al., 2012), time (S. Michelmann, et al., 2016; Staudigl, et
67 al., 2015), and time-frequency (Staresina, et al., 2016; Yaffe, et al., 2014). These studies
68 demonstrate the general importance of neural pattern reinstatement for memory retrieval,
69 however, we know little about the functional relevance of neural pattern reinstatement for
70 memory and its involvement in Encoding Specificity (or Transfer Appropriate Processing). This
71 is because there are hardly any studies which have tested the impact of neural pattern
72 reinstatement on memory retrieval in the face of retrieval cues which match or do not match the
73 encoding modality.

74 Two predictions can be made as to how neural pattern reinstatement impacts on memory in such
75 matching and non-matching retrieval contexts. The first prediction is that the reinstatement of the
76 original encoding pattern during retrieval is always beneficial for memory; regardless of a match
77 between the retrieval and study contexts. In such a scenario, reactivation of the neural pattern
78 containing the study episode does not support Encoding Specificity. A contrasting second
79 prediction is that the reinstatement of encoding patterns is only beneficial for retrieval when the
80 study and retrieval contexts match; if the study and retrieval context do not match, then
81 reinstatement of encoding patterns might even be detrimental. In this case, the reactivated
82 encoding pattern does not match the retrieval cue. This conflict could bias the memory decision
83 towards a miss, i.e., judging an old item as new. In this second scenario, reactivation of the
84 neural pattern containing the study episode would support Encoding Specificity. To the best of
85 our knowledge, only one such study has been conducted which investigated neural pattern
86 reinstatement in a paradigm using background movies as matching/non-matching contexts

87 (Staudigl, et al., 2015). Indeed, in this prior study we confirmed the second prediction, showing
88 that memory benefitted from neural pattern reinstatement only when the encoding and retrieval
89 contexts matched but suffered from reinstatement when the contexts did not match. This study
90 can be seen as a first evidence that neural patterns established during encoding resonate with a
91 retrieval cue, and that this resonance has a functional relevance for memory retrieval. This result
92 therefore serves as a neural explanation for the Encoding Specificity Principle (or Transfer
93 Appropriate Processing). However, if this reactivation of neural patterns is a general mechanism
94 underlying Encoding Specificity, then we should be able to expand these results to different
95 match/mismatch manipulations. It is therefore necessary to investigate specific predictions about
96 neural pattern reactivation in different matching and mismatching encoding and testing
97 scenarios. Specifically, it is important to show that the interaction between neural pattern
98 reactivation and encoding-retrieval overlap is not only observed in visual contextual overlap (as
99 tested in Staudigl et al., 2015) but is also observed in other sensory modalities. Therefore, we
100 here investigate neural pattern reactivation in a memory paradigm using a sensory modality
101 match manipulation (Mulligan and Osborn, 2009) in which the items are studied and retrieved
102 either visually or aurally (Figures 1 & 2). We demonstrate the effects of the modality match on
103 memory performance in a simple computational model (Figure 2), illustrating our hypothesis in
104 support of Encoding Specificity.

105 Neural pattern reinstatement can be measured in various ways with various recording techniques.
106 Here we used MEG and focussed on the reinstatement of temporal patterns, as measured with
107 phase in lower frequencies (<40 Hz). We chose this approach over other approaches (i.e. based
108 on power distribution across sensors; Jafarpour, et al. (2014); Fuentemilla, Penny, Cashdollar,
109 Bunzeck, & Düzel (2010)) because previous studies showed that phase based temporal

110 similarity measures effectively captures the reactivation of temporal patterns in memory (S.
111 Michelmann, et al., 2016; Sebastian Michelmann, Bowman, et al., 2018; Sebastian Michelmann,
112 Staresina, et al., 2018; Schreiner, et al., 2018; Staudigl, et al., 2015). We hypothesize to find
113 higher temporal pattern similarity for successfully remembered items compared to forgotten
114 items when the encoding and retrieval modalities match, and a reversal of this pattern when the
115 encoding and retrieval modalities do not match. To foreshadow our findings, on a behavioural
116 level we replicated the modality match effect (Mulligan and Osborn, 2009) for aurally encoded
117 words, but not for visually encoded words (Figure 3). Therefore, we analysed the MEG data
118 separately based on encoding modality and expected the above described interaction pattern only
119 for the condition which showed a behavioural effect (i.e. for aurally encoded words, Figure 1B).

120

121

122 **Methods**

123 **Ethics statement**

124 The study was approved by the Institutional Review Board of the University of Konstanz. All
125 participants gave written informed consent before the start of experiment in accordance with the
126 Declaration of Helsinki.

127

128 **Participants**

129 24 participants (between 19 and 26 years old; mean age = 22 years; 17 female; 21 right-handed)
130 were recruited for study. After excluding four participants (technical problems, excessive
131 environmental noise), data from 20 participants are presented here. Participants received course

132 credits or monetary compensation for participation. All participants were German native
133 speakers and reported no history of neurological disease and normal or corrected-to-normal
134 vision.

135 Parts of this data have been published in (Staudigl and Hanslmayr, 2013) and (Westner, Dalal,
136 Hanslmayr, & Staudigl, 2018), with respect to independent research questions and analyses
137 (Staudigl & Hanslmayr, 2013: subsequent memory effects, study phase data only; Westner,
138 Dalal, Hanslmayr & Staudigl, 2018: classification of stimulus modality, study phase data only).

139

140 **Procedure**

141 The experiment consisted of a study and a test phase. An outline of the procedure is depicted in
142 Figure 1A. Before the start of the experiment, participants were instructed to count the syllables
143 of each presented word and indicate via button press whether the word had two or more / less
144 than two syllables. Participants were not instructed about the subsequent memory test, i.e.,
145 incidental encoding can be assumed. A short practice run ensured that the participants
146 understood the task requirements.

147 During the study phase, words were presented in one of two modalities. In the visual encoding
148 condition, words were projected on a screen. In the auditory encoding condition, vocal
149 recordings of the words were presented via nonferromagnetic tubes to both ears, whilst the
150 fixation cross remained on the screen. The duration of the word presentation was determined by
151 the individual duration of the respective audio file, i.e., the time to pronounce the word (i.e.
152 “dog” was presented for a shorter duration than “table”; mean duration = 697 ms, s.d. = 119 ms).
153 Words were followed by a fixation cross. The duration of the word and fixation cross added up
154 to 2000 ms. Thereafter, a question mark prompted the subject’s response in the syllable counting

155 task. Participants were instructed before the start of the experiment to count the syllables of the
156 word and indicate via button press whether the word had two syllables. The presentation of the
157 question mark was either ended by the subject's button press or after a maximum duration of
158 1500 ms. A fixation cross (variable duration between 1000 and 1500 ms) preceded each word.
159 After the study phase, participants performed a distracter task during which they counted
160 backwards (in steps of three from a three-digit number) for 45 seconds.
161 After the distracter task, participants were informed about the upcoming, surprise recognition
162 memory test. Participants were instructed to indicate their confidence on whether the item was
163 old (presented during the study phase) or new (not presented during the study phase) on a six-
164 point scale ranging from 'very sure old' to 'very sure new'. A short practice run ensured that the
165 participants understood the task requirements.
166 During the test phase, words were presented with individual duration (determined by the duration
167 of the respective audio file), followed by a fixation cross (summed duration of word and fixation
168 cross = 2000 ms), followed by a stimulus picture depicting the response option. This stimulus
169 prompted the participants' response indicating their confidence on whether they recognized the
170 word as old or new, by pressing one out of six specified buttons on the response panel. The
171 stimulus picture prompting the response was shown until the participants gave a response. A
172 fixation cross (variable duration between 750 and 1250 ms) preceded each word.

173

174 **Design and materials**

175 420 unrelated German nouns were grouped into three lists with 140 words, each. Half of each
176 list's words had two syllables, the other half had one, three or four syllables. Two lists were
177 presented during the study phase (280 old items). Half of these words were presented visually,

178 the other half aurally. The assignment of words to modality was counterbalanced across
179 participants. At test, the 280 old items intermixed with the 140 words from the remaining list
180 (new items) were presented. Half of the old words were presented in the same modality (match
181 condition), the other half in the different modality (mismatch condition) as during the study
182 phase. Half of the new items were presented visually, the other half aurally.

183 The assignment of the lists to either study or test phase was counterbalanced across participants.
184 For half of the participants, the confidence judgment during recognition test ranged from ‘very
185 sure old’ (1) to ‘very sure new’ (6), for the other half from ‘very sure new’ (1) to ‘very sure old’
186 (6), thereby counterbalancing the response lateralization across subjects. Items were presented in
187 a random order, with the constraint that not more than five words of the same modality (visual,
188 auditory) and not more than five words from the same condition (match, mismatch) were
189 presented sequentially.

190 The assignment of mismatch trials to either the auditory or visual mismatch condition (see Fig.
191 1b) was based on the modality of the study phase (i.e., mismatch trials were not averaged across
192 conditions). Presenting a word aurally versus visually in the study phase results in modality-
193 specific encoding patterns of neuronal activity. To investigate how the reactivation of these
194 modality-specific neuronal patterns would affect retrieval during the test phase, it is important to
195 keep the encoding modality constant and vary the modality of the retrieval cue (match or
196 mismatch). Moreover, by keeping separate mismatch conditions for each we retained balanced
197 trial numbers, thus keeping the signal-to-noise ratio for match and mismatch conditions constant.

198

199 **Simulation**

200 A simple computational model was generated to illustrate the opposing effects that the
201 reactivation of neural patterns may have on memory performance in match and mismatch
202 conditions. The model was inspired by a theoretical paper by E. Tulving (Tulving, 1983) who
203 envisioned an early resonance process, termed “Ephory” which can be described
204 mathematically via a correlation between a stored engram and a retrieval cue and which inputs
205 into the retrieval process. The simulation was programmed in MATLAB (version R2016a) and is
206 a slightly modified version of a previous simulation published in (Staudigl, et al., 2015). The
207 code for the simulation is available on https://github.com/hanslmayr/Audivis_Simulation. The
208 model is divided into two layers, a semantic layer and a sensory layer, to simulate item meaning
209 and the sensory modality in which an item is presented. Therefore, the sensory layer is further
210 divided into auditory and visual units (see Figure 2). The semantic layer has 12 units; the sensory
211 layer had 6 units for visual and 6 units for auditory patterns. Item patterns were expressed by a
212 combination of 3 activated units on each layer (see Figure 2); 100 patterns were generated to
213 simulate encoding and retrieval of 100 items. Thereby, each item was represented by a unique
214 combination of a 3 unit pattern in a semantic layer and a 3 unit pattern in a sensory layer. These
215 patterns were expressed in forms of 3 by 4 matrices, containing zeros for non-activated units and
216 ones for activated units (see Figure 2).

217 Memory retrieval was simulated via an interaction, i.e. correlation, between a *reactivated pattern*
218 (R) and a *cued pattern* (C) (Tulving, 1983). The simulation was calculated individually for each
219 item, resulting in 100 trials. Within each trial, the reactivated pattern was first calculated
220 separately for the semantic and the sensory layer. On the semantic layer, the reactivated semantic
221 pattern (R_{sem}) was simply assumed to be the same as the cued pattern (C_{sem}) with a constant small
222 amount of white noise (range 0 to 0.1). No difference was assumed between match and mismatch

223 conditions, as in our experiment items were identical on a semantic level between match and
 224 mismatch conditions. On the sensory layer, we calculated the reactivated pattern (R_{sens}) by taking
 225 the original sensory pattern and adding white noise onto it. The strength of noise was controlled
 226 by a reactivation parameter (high vs. low reactivation) in order to simulate the effects of strength
 227 of reactivation on memory performance (i.e. high levels of noise result in low levels of
 228 reactivation). The cued pattern (C_{sens}) on the sensory layer varied between match and mismatch
 229 conditions. For the match condition, C_{sens} was the original pattern in the respective sensory layer
 230 in which the item has been encoded (i.e. auditory layer for aurally encoded words). Therefore,
 231 for match conditions C_{sens} overlapped with R_{sens} , with the strength of this overlap depending on
 232 the noise parameter which controls the strength of reactivation. For mismatch conditions, C_{sens}
 233 was taken from different units of the sensory layer (i.e. visual units for aurally encoded words).
 234 Therefore, for mismatch conditions C_{sens} never overlapped with R_{sens} . The overlap for a given
 235 trial was operationalized as the average across the fisher-z transformed 2d correlations (rz)
 236 between the cued and reactivated patterns on the semantic and sensory layers as per the below
 237 equation. Memory (Mem) performance is assumed to be a readout of the overlap:

238

$$Mem = \frac{rz(C_{sem}, R_{sem}) + rz(C_{sens}, R_{sens})}{2}$$

239

240 **Data acquisition and preprocessing**

241 MEG data was recorded with a whole-brain 148-channel magnetometer system (MAGNESTM
 242 2500 WH, 4D Neuroimaging, San Diego, USA) inside a magnetically shielded room from
 243 participants in supine position. The data was continuously recorded at a sampling rate of 678.17

244 Hz and bandwidth of 0:1-200 Hz. Preprocessing of the data was done using the fieldtrip toolbox
245 (Oostenveld, Fries, Maris, & Schoffelen, 2011), an open-source MATLAB toolbox for MEEG
246 data analysis. Data from the study and test phase was epoched into single trials, with epochs
247 ranging from 1500 ms prior to the onset of word presentation to 4000 ms after onset of word
248 presentation. Trials were visually inspected for artefacts, to reject contaminated trials. Thereafter,
249 independent component analysis (ICA) was used to correct for blinks, eye movements, and
250 cardiac artefacts. On average, 3 (std = .79) components were rejected manually in the study
251 phase, and 5.2 (std = 3.72) components were rejected in the test phase.

252 After artefact rejection, 54.95 (std = 6.1) trials remained on average in the auditory match
253 condition (remembered trials: mean = 38.65, std= 8.2; forgotten trials: mean = 16.3 std= 6.59)
254 and 55.4 (std = 6.15) in the auditory mismatch condition (remembered trials: mean = 35.1, std=
255 7.59; forgotten trials: mean = 20.3 std= 4.75). In the visual match condition, 55.3 (std= 6.3) trials
256 remained (remembered trials: mean = 35, std= 8.06; forgotten trials: mean = 20.3 std= 6.37) and
257 53.4 (std = 6.7) in the visual mismatch condition (remembered trials: mean = 32.85, std= 7.35;
258 forgotten trials: mean = 20.5 std= 5.66).

259
260 All trials remaining after artefact inspection were categorized according to the behavioural
261 performance of each participant's during the recognition test phase. Trials including old items
262 that were confidently judged as old (responses 1, 2, and 3) constituted remembered trials, the
263 remaining trials including old items were classified as forgotten trials, in both the study and the
264 test phase. Trials including new items that were confidently judged as being new (responses 4, 5,
265 and 6) constituted correct rejections, the remaining trials including new items were classified as
266 false alarms.

267

268 **Similarity analysis**

269 In order to identify reinstatement of neuronal patterns from encoding during retrieval, similarity
270 in neuromagnetic activity between words presented at study and test was assessed. Based on
271 previous findings (S. Michelmann, et al., 2016; Staudigl, et al., 2015), we focused on similarity
272 in oscillatory phase, using the pairwise phase consistency index (PPC; (Vinck, van Wingerden,
273 Womelsdorf, Fries, & Pennartz, 2010). PPC estimates the phase consistency between two
274 separate signals across trials, quantifying the extent of a consistent phase relationship among
275 them. Compared to other measures of phase consistency (e.g., phase-locking value), PPC is
276 advantageous since it is not biased by the number of trials. As a consequence of the
277 unbiasedness, the PPC can, however, have negative values (Vinck, et al., 2010).

278 In order to provide the necessary phase information for the computation of the PPC, time-
279 frequency representations of the data were computed by a sliding time window approach with a
280 window length of 0.5 s in steps of 50 ms across the data. After multiplying a hanning taper to
281 each window, the Fourier transformation was calculated for frequencies between 4 and 40 Hz in
282 steps of 2 Hz.

283 The PPC was calculated between each of the time-frequency bins in the study phase and the
284 corresponding time-frequency bins in the test phase, separately for remembered and forgotten
285 trials, match and mismatch condition, and auditory and visual encoding condition.

286

287 **Statistics**

288 Statistical quantification of the data was performed by a cluster-based nonparametric
289 permutation approach (Maris and Oostenveld, 2007) identifying clusters of activity on the basis

290 of rejecting the null hypothesis while controlling for multiple comparisons over sensors, time-
291 points and frequencies. For each time and frequency bin at each sensor, a test statistic was
292 calculated (10,000 permutations), based on a paired samples t-test comparing the difference in
293 PCC in the match condition (remembered minus forgotten trials) to the difference in PPC in the
294 mismatch condition (remembered minus forgotten trials; see Figure 1b).

295 T-values above the cluster-forming threshold ($p < 0.05$, two-sided t-test) were clustered based on
296 adjacency in time, frequency and space (a minimum of 2 adjacent sensors was required for
297 forming a cluster). T-statistics were summed in each cluster and compared against the
298 distribution of maximal clusters provided by the permutation approach, using the Monte Carlo
299 method for randomly assigning the differences (remembered minus forgotten) to conditions
300 (match, mismatch). Only the cluster with the largest summed value was considered and tested
301 against the permutation distribution. The null-hypothesis that the match and mismatch condition
302 showed no difference in PPC was rejected at an alpha-level of 0.05 (two-tailed).

303

304

305 **Results**

306 **Behavioural results**

307 A summary of the behavioural results is depicted in Figure 3. Averaged across modality
308 conditions, participants correctly recognized significantly more words ($t_{19} = 3.56$, $p < 0.005$) in
309 the match (mean = .661, SE = .023) than the mismatch condition (mean = .621, SE = .020). The
310 interaction between modality (auditory vs. visual) and test condition (match vs. mismatch) was
311 not significant ($F_{1,19} = 2.72$, $p > .115$).

312 In the auditory encoding condition, participants correctly recognized significantly more words in
313 the match (mean = .695, SE = .025) than in the mismatch (mean = .63, SE = .023) condition (t_{19}
314 = 3.55, $p < .005$). No significant difference between correctly recognized words in the match
315 (mean = .626, SE = .024) and the mismatch (mean = .612, SE = .024) condition was found for
316 visually encoded items ($t_{19} = .73$, $p > 0.475$). Note that this pattern of results cannot be
317 interpreted as a modality x condition interaction effect (see Nieuwenhuis, Forstmann, &
318 Wagenmakers, 2011, for an important discussion on interaction effects).

319 The false alarm rate was not significantly different ($t_{19} = -0.62$, $p > .54$) for items presented
320 visually (mean = .26, SE = .027) or aurally (mean = .27, SE = .025) during test.

321 When only including the high confidence judgements (“very sure old”), the interaction between
322 modality (auditory vs. visual) and test condition (match vs. mismatch) was significant ($F_{1,19} =$
323 10.79, $p < .005$). In the auditory encoding condition, participants correctly recognized
324 significantly more words in the match (mean = .384, SE = .038) than in the mismatch (mean =
325 .307, SE = .035) condition ($t_{19} = 3.70$, $p < .005$). No significant difference between correctly
326 recognized words in the match (mean = .285, SE = .032) and the mismatch (mean = .311, SE =
327 .032) condition was found for visually encoded items ($t_{19} = -1.43$, $p > 0.168$).

328

329 **Simulation results**

330 We created a simple computational model to formalize our hypotheses and to illustrate the
331 impact of neural pattern reactivation on memory performance for match and mismatch
332 conditions. The results of this model are shown in Figure 2. If the modality of the retrieval cue
333 matches the encoding modality (Figure 2a), high levels of sensory reactivation lead to a strong
334 resonance, i.e. a better memory performance. On the other hand, if the modality of the retrieval

335 cue does not match the modality of the encoded pattern, then high levels of sensory reactivation
336 lead to lower resonance, i.e. worse memory performance (Figure 2b). This latter effect arises
337 because in the mismatch modality the patterns of the engram and the cued patterns never overlap
338 as they are represented in different units. Reactivation of a sensory trace in the mismatch
339 condition therefore leads to a negative correlation which then reduces the overall correlation
340 between the cue and the reactivated pattern. This simple model illustrates what we should expect
341 to find if neural pattern reactivation underlies the encoding specificity principle. That is, high
342 levels of reactivation for remembered trials in the match condition, but low levels of reactivation
343 for remembered trials in the mismatch condition.

344

345 **Reinstatement of auditory temporal patterns interacts with modality match**

346 In order to identify memory reinstatement of temporal patterns from encoding during retrieval,
347 similarity in neuromagnetic activity between words presented at study and test was assessed
348 using the pairwise phase similarity (S. Michelmann, et al., 2016). Given the asymmetric
349 behavioural pattern, i.e. a modality match effect was only observed for aurally encoded words,
350 the analysis was carried out separately for visually and aurally encoded words.

351 In the auditory encoding condition, cluster-based nonparametric statistics yielded a significant
352 interaction effect ($p_{\text{cluster}} < .05$), indicating that the difference in the match condition
353 (remembered – forgotten) was reliably higher than in the mismatch condition (remembered –
354 forgotten) at 6-8 Hz between 0.15 and .2 seconds after word onset (Figure 4a). Figure 4b depicts
355 a topography of the interaction effect, highlighting left central sensors contributing to the
356 significant cluster.

357 Post-hoc t-tests revealed that the neuronal similarity was higher for the remembered than the
358 forgotten words in the match condition for ($t_{19} = 5.02$, $p < .0001$), whereas in the mismatch
359 condition, similarity was higher for the forgotten than the remembered words ($t_{19} = 2.11$, $p < .05$,
360 see Figure 4b). Comparing only remembered words revealed that the neuronal similarity was
361 higher in the match than in the mismatch condition ($t_{19} = 2.46$, $p < .05$). It should be noted that
362 this post-hoc analysis is statistically biased by selectively averaging across those channels, time
363 and frequency bins that show a significant interaction. Nevertheless, this post-hoc analysis adds
364 information as it shows that the interaction is not just driven by a difference in one condition, but
365 by opposing differences between remembered and forgotten items in both conditions.

366 In another post-hoc analysis, we included high confidence trials (“sure old” responses) in the
367 remembered condition only (HCrem). When averaging across the time and frequency bins that
368 showed a significant interaction in the previous analysis, a very similar topography was found
369 (Fig 5, left). When averaging across the channels, time and frequency bins that showed a
370 significant interaction in the previous analysis, the interaction effect for the HCrem items
371 resembled the pattern found in the original analysis: The interaction (match/mismatch vs.
372 remembered/forgotten) was significant ($F_{1,19}=9.76$, $p < 0.01$), as well as the comparison between
373 HCrem and forgotten items in the match condition ($t_{19} = 3.72$, $p < .005$). The comparison
374 between HCrem and forgotten items in the mismatch condition was not significant ($t_{19} = -1.13$, p
375 $> .27$), as well as the comparison between HCrem in the match and the mismatch condition ($t_{19} =$
376 1.39 , $p > .18$).

377

378 In the visual condition, there were no significant interaction effects when comparing the
379 difference (remembered – forgotten) in the match condition to the difference (remembered –
380 forgotten) in the mismatch condition (all cluster p's > .59).

381 When remembered versus forgotten items were compared irrespective of match / mismatch
382 condition, no significant effects were found in the auditory (p cluster > .08) nor in the visual
383 condition (p cluster > .16).

384

385

386

387 **Discussion**

388 In the current study we investigated how the reactivation of encoding patterns interacts with
389 memory in the face of retrieval cues which match or do not match the encoding modality. For
390 aurally encoded words, we show that reactivation of encoding patterns is related to opposing
391 memory outcomes; depending on whether the retrieval cue matches the encoding modality or
392 not. Specifically, reactivation of a sensory encoding pattern is beneficial for memory when the
393 retrieval cue matches the encoding modality, but is detrimental when the cue does not match the
394 encoding modality. Together with our previous findings (Staudigl, et al., 2015), these results
395 provide insights into the neural basis underlying a classic effect in cognitive psychology, i.e.
396 Encoding Specificity or Transfer Appropriate Processing (Morris, et al., 1977; Tulving and
397 Thomson, 1973): the more the retrieval cue overlaps with the encoded pattern, i.e. the stronger
398 the two resonate, the more likely it is that the item will be recognized as old (Rugg, et al., 2008).
399 Paradoxically, when the retrieval cue is presented in a different sensory modality than in which

400 the item has been encoded, reactivation of sensory patterns was related to decreased memory
401 performance. This pattern is in line with the outcome of a simple model which illustrated our
402 results on a neural and behavioural level: the mismatch between the reactivated sensory pattern
403 (i.e. “dog” in auditory layer) and the sensory pattern provided by the retrieval cue (i.e. “dog”
404 visually presented) decreases the overlap (or resonance) between the cue and the reactivated
405 pattern, and, thereby, the memory performance. This decrease is even more pronounced in case
406 of a strongly reactivated memory trace.

407 Neural evidence consistent with Encoding Specificity comes from fMRI (Park and Rugg, 2008)
408 and ERP studies (Bauch and Otten, 2012). These studies show that the neural correlates of
409 successful encoding vary depending on whether the memory is later tested with cues that match
410 or do not match the encoding modality (Park and Rugg, 2008). We here add to this neural
411 evidence by using a temporal pattern similarity approach and show that reactivation of neural
412 patterns established at encoding has opposing effects on memory depending on how the memory
413 is cued. One advantage of the here used approach is that it returns a time-resolved measure of
414 memory reactivation, which allows to infer whether reactivation is an early process leading up
415 to a memory judgement or whether it is a later by-product of a memory judgement (i.e. imagery,
416 or retrieval monitoring). The early time window of reactivation observed here (i.e. 150 – 200 ms)
417 supports the former view and suggests an early resonance process between a memory cue and a
418 stored engram which occurs before the memory decision is being made, which has been termed
419 Ecphory (Tulving, 1983). This finding is consistent with a larger body of studies describing
420 similar early reactivation effects (Jafarpour, et al., 2014; Waldhauser, Braun, & Hanslmayr,
421 2016; Wimber, Maass, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012, but see Lewis,
422 Schriefers, Bastiaansen, & Schoffelen, 2018; Price and Johnson, 2018).

423 Interestingly, on a behavioural level the observed modality match effects were asymmetric, i.e. a
424 modality match effect was observed only for aurally encoded words but not for visually encoded
425 words (albeit it should be acknowledged that there was no significant 2-way interaction between
426 match/mismatch and modality). Consistent with this asymmetric pattern, only aurally encoded
427 items showed an interaction effect in terms of neural pattern reactivation with modality match,
428 whereas no such effect was obtained for visually encoded items. A possible post-hoc explanation
429 for this asymmetry is that the visual presentation of words automatically evokes auditory patterns
430 encoded by the participants. This would be consistent with reports of high levels of auditory
431 cortex activation typically observed during reading, and in line with the idea that auditory cortex
432 is part of the brain's "reading network" (Wandell and Le, 2017). This activation of auditory
433 patterns might have been further promoted by the here used encoding strategy, i.e. syllable
434 counting which arguably enforces subjects to covertly pronounce the word. In such a scenario,
435 for a visually encoded word, an auditory cue is just as effective as a visual cue because the
436 engram contains both patterns. Consistent with this explanation, a previous study (Mulligan and
437 Osborn, 2009) which reported modality match effects for visually *and* aurally encoded words
438 used a different encoding strategy, i.e. intentional encoding (as opposed to syllable counting and
439 incidental encoding employed in our study). On a more general level, these considerations
440 highlight the importance of the cognitive processes carried out at encoding and retrieval which
441 determine memory effects observed on a behavioural and neural level (Hanslmayr and Staudigl,
442 2014; Rugg, et al., 2008).

443 The here observed reactivation of auditory patterns occurred in a frequency range of 6-8 Hz. This
444 frequency range perfectly matches a previous study where we found that dynamic auditory
445 patterns are encoded in the phase of a 6-8 Hz oscillation (S. Michelmann, et al., 2016; Sebastian

446 Michelmann, Bowman, et al., 2018; Schreiner, et al., 2018). This result is also in line with
447 another study showing that auditory stimuli can be decoded from neural phase patterns at 4-8 Hz
448 (Ng, Logothetis, & Kayser, 2013). This result is, however, in contrast to a previous study
449 (Staudigl, et al., 2015) investigating match-mismatch with background movies, where we found
450 reactivated patterns at a higher frequency range (i.e. 30 Hz). This difference could be either due
451 to the different sensory modalities of the stimuli between the two studies (i.e. auditory vs visual),
452 or could be due to slightly different analysis approaches. In contrast to Staudigl et al. 2015, we
453 here used pairwise phase consistency (PPC) as we did in Michelmann et al (2016, 2018) which
454 has the advantage of resulting in a time-resolved measure of Temporal Pattern Similarity.
455 Together with previous studies (S. Michelmann, et al., 2016; Sebastian Michelmann, Bowman, et
456 al., 2018; Ng, et al., 2013; Schreiner, et al., 2018) these results suggest a general role of 6-8 Hz
457 oscillations for coding auditory information not only on a perceptual level, but also in memory.

458 **Conclusion**

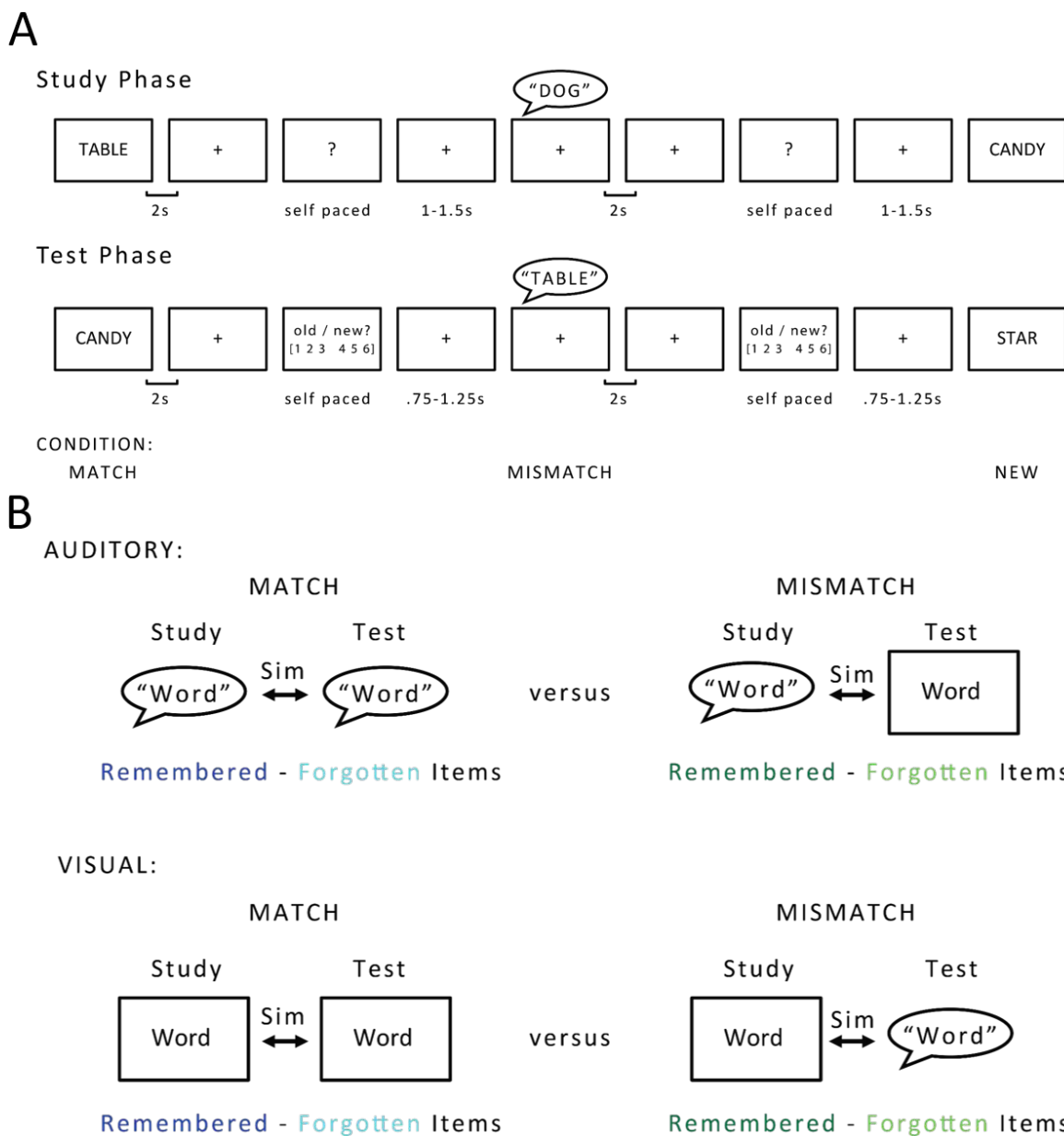
459 The encoding specificity principle or transfer appropriate processing are classic frameworks
460 which have influenced memory research for decades. In their seminal paper published in 1973,
461 Tulving and Thomson describe the basic ideas of Encoding Specificity but also state:

462 *„The terms are ill defined, and the concepts do not explain too much at this time. Yet they serve*
463 *to remind us that something else besides the properties of a presented item determines how well*
464 *the item is remembered and that an important research problem is to find what this something*
465 *else is and how it works“ (Tulving and Thomson, 1973).*

466 More than 4 decades later we still know little about the mechanisms underlying the encoding
467 specificity principle. In neural terms, the encoding specificity principle can be expressed as a

468 resonance process between a cue and a stored engram, whereby the overlap between the two
469 determines whether a memory can be retrieved or not (Rugg, et al., 2008; Tulving, 1983). We
470 here show that the strength of reactivation of that memory trace plays a central role in this
471 process and thus is a critical ingredient underlying Encoding Specificity (or Transfer Appropriate
472 Processing). We hope that future studies pick up on these ideas using multivariate analysis tools
473 which allow to quantify the reactivation of stored memory traces (i.e. the engrams) using
474 standard neuroimaging tools such as EEG, MEG or fMRI.

475



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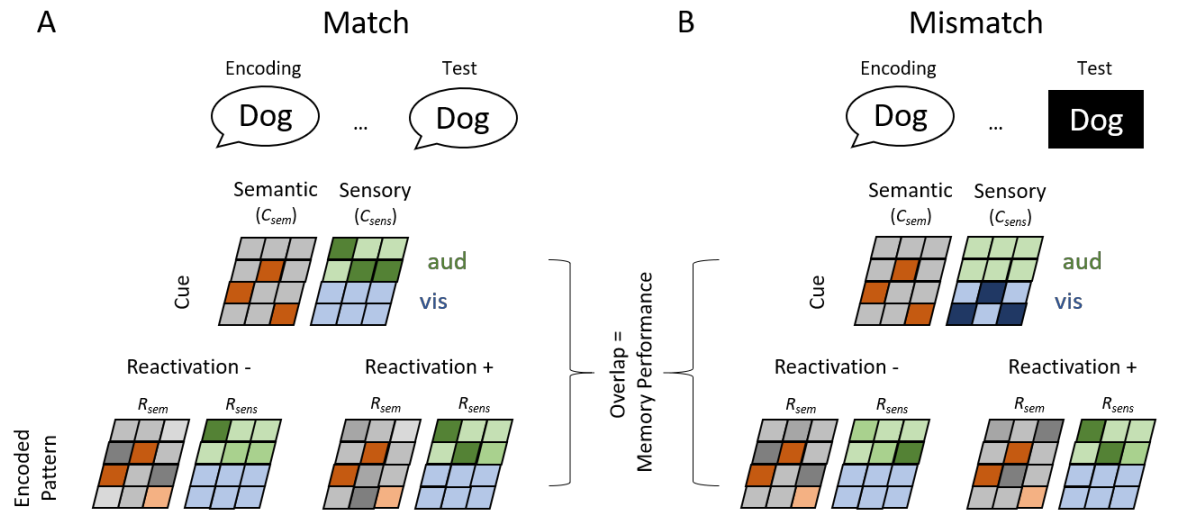
478 **Figure 1.**

479 Experimental Procedure and analysis rationale. A) Procedure. In the study phase, words were
 480 either presented visually or aurally (indicated by the speech bubble). Duration of presentation
 481 was adjusted individually for each word to match the duration of the audio file. The combined
 482 presentation time of the word and fixation cross was 2 always seconds. Participants were

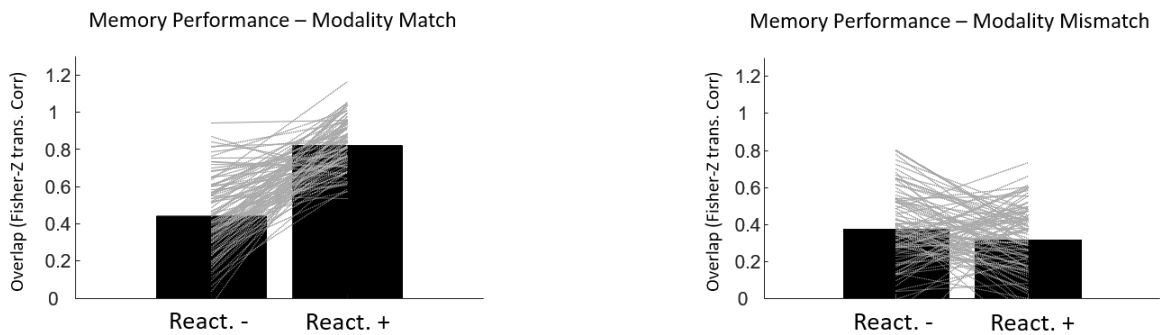
483 instructed to count the syllables (two or more/less than two) of each word and respond during the
484 question mark. In the test phase, old words were either presented in the same (match condition)
485 or different (mismatch condition) modality as during the study phase. Old words were randomly
486 intermixed with new words, and participants were asked to judge their confidence as to whether
487 the word was old or new on a six-point scale, ranging from ‘very sure old’ (1) to ‘very sure new’
488 (6). B) Analysis rationale. Temporal Pattern Similarity was computed for word pairs presented
489 during study and test. Similarity differences between remembered and forgotten words were
490 compared between the match and mismatch condition, separately for the auditory and the visual
491 condition.

492

493



Results Simulation

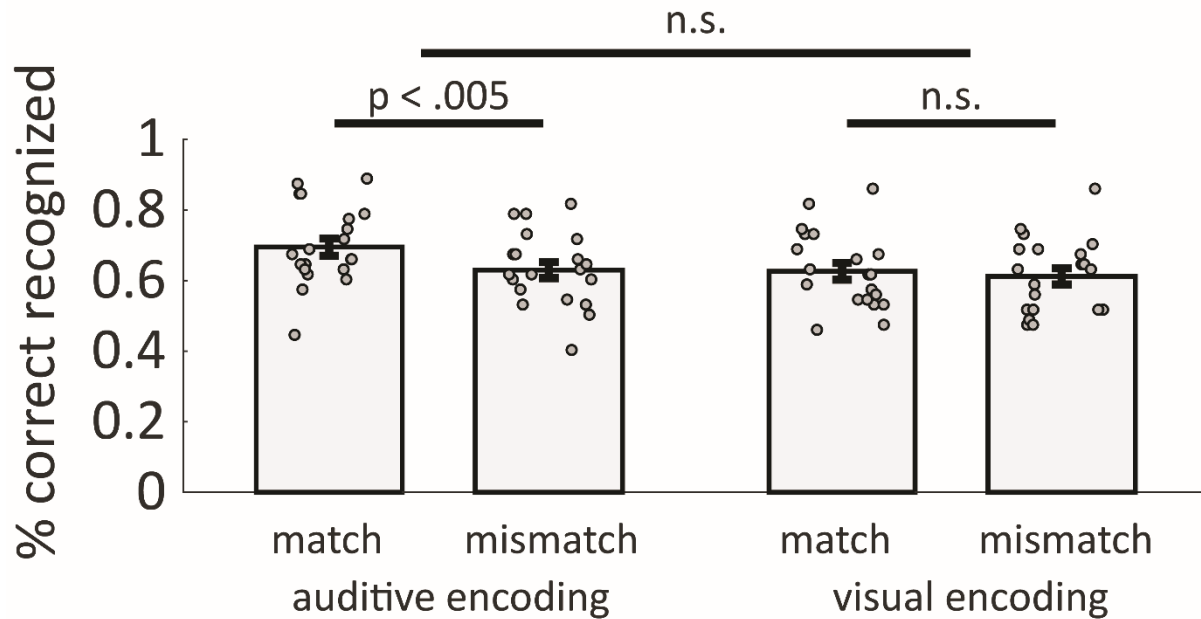


494

495 **Figure 2.** The architecture of a simple computational model (top panel) and results of the
 496 simulation (bottom panel) are shown for Match (A) and Mismatch (B) conditions. Individual
 497 patterns were generated on a semantic and a sensory layer to represent cued and encoded item
 498 patterns. The sensory layer was divided into visual and auditory units. Memory performance was
 499 conceived of as the overlap between a cued pattern (C_{sem} , C_{sens}) and a reactivated pattern (R_{sem} ,
 500 R_{sens}) as calculated with 2d correlations. These correlations were averaged across the two layers.
 501 The bottom panel shows the overlap averaged across simulation runs (bar plots) and individual
 502 trials (grey lines) for high and low reactivation levels (React.+ and React.-, respectively). 100
 503 simulation runs per condition and reactivation level were carried out.

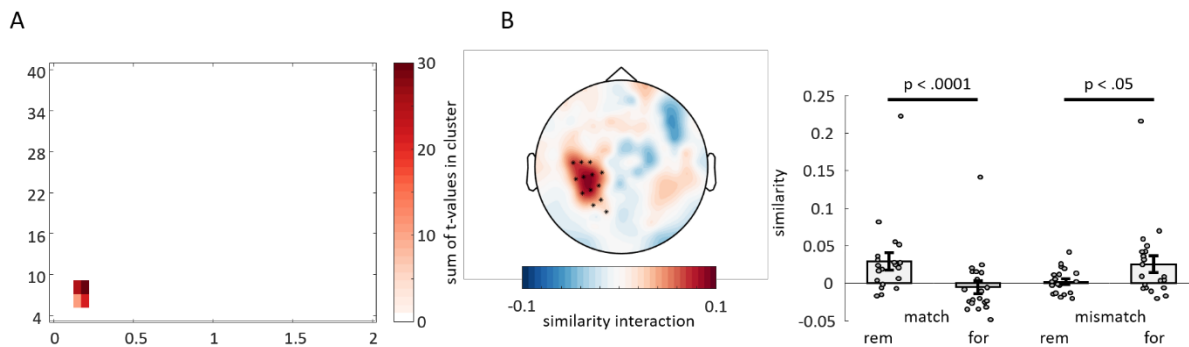
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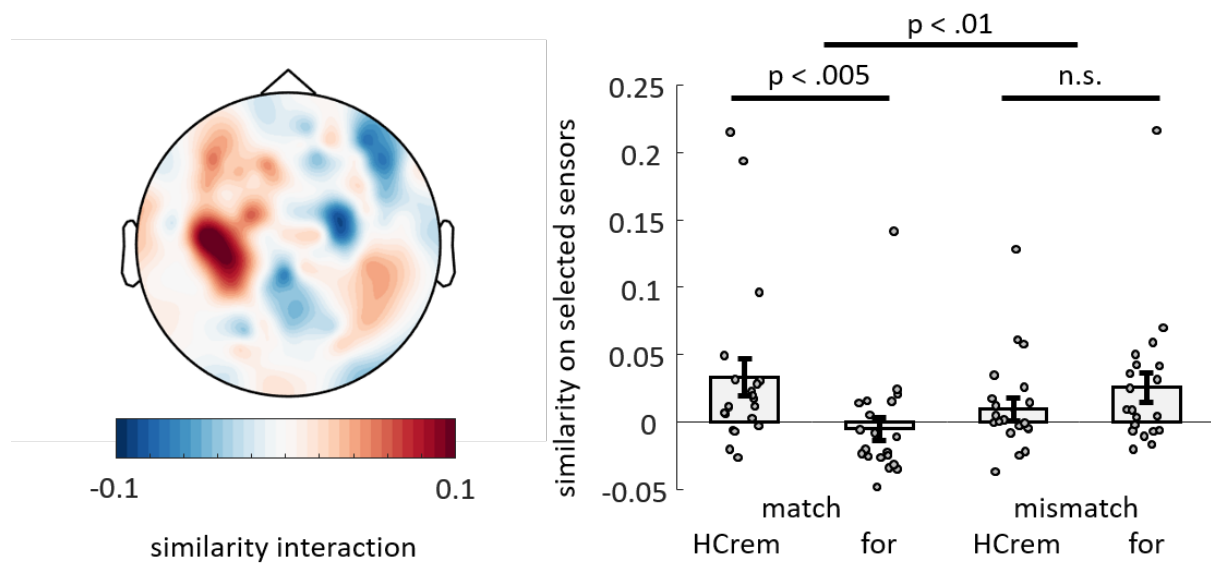
507 **Figure 3.** Behavioural results. Recognition performance in the match and mismatch condition as
508 a function of auditory (left) and visual (right) encoding. A modality match effect was observed
509 only for the auditory encoding condition ($p < .005$). Dots represent individual data points, errors
510 bars depict S.E.



511

512 **Figure 4.** Interaction effect in the auditory condition. A) Significant interaction (p cluster $< .05$)
513 between the match (remembered – forgotten) and the mismatch (remembered – forgotten)
514 condition, at 6-8 Hz and .15-.2 s after word onset. B) Left: Topography of the interaction effect
515 ([PPC match remembered – PPC match forgotten] - [PPC mismatch remembered – PPC

516 mismatch forgotten]), averaged across time and frequency depicted in A. Sensors contributing to
 517 the significant interaction are highlighted. Right: Similarity (PPC) for the remembered and
 518 forgotten words, in the match and mismatch condition, respectively, as averaged across time
 519 (.15-.2 s), frequencies (6-8 Hz) and sensors highlighted in the topography. Dots represent
 520 individual data points, errors bars depict S.E.
 521



522
 523 **Figure 5.** High confidence – remembered words (HCrem) in the auditory condition. A) Left:
 524 Topography of the interaction ([PPC match HCrem – PPC match forgotten] - [PPC mismatch
 525 HCrem – PPC mismatch forgotten]), averaged across time and frequency depicted in Figure 4A.
 526 Right: Similarity (PPC) for HCrem and forgotten words, in the match and mismatch condition,
 527 respectively, as averaged across time (.15-.2 s), frequencies (6-8 Hz) and sensors highlighted in
 528 the topography of Figure 4b. Dots represent individual data points, errors bars depict S.E.

529

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537 awards/grants/wolfson-research-merit/](https://royalsociety.org/grants-schemes-awards/grants/wolfson-research-merit/)) to SH.

538

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