

Accessing forgotten memory traces from long-term memory via visual movements

Estela Camara and Lluís Fuentemilla

Journal Name:	Frontiers in Human Neuroscience
ISSN:	1662-5161
Article type:	Original Research Article
Received on:	28 Aug 2014
Accepted on:	31 Oct 2014
Provisional PDF published on:	31 Oct 2014
www.frontiersin.org :	www.frontiersin.org
Citation:	Camara E and Fuentemilla L(2014) Accessing forgotten memory traces from long-term memory via visual movements. <i>Front. Hum. Neurosci.</i> 8:930. doi:10.3389/fnhum.2014.00930
Copyright statement:	© 2014 Camara and Fuentemilla. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY) . The use, distribution and reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

This Provisional PDF corresponds to the article as it appeared upon acceptance, after rigorous peer-review. Fully formatted PDF and full text (HTML) versions will be made available soon.

1 **Accessing forgotten memory traces from long-term memory**
2 **via visual movements**

3
4 Estela Càmara¹ & Lluís Fuentemilla^{1,2}

5
6 ¹Cognition and Brain Plasticity Unit. Institute of Biomedical Research of Bellvitge
7 (IDIBELL)

8 ²Department of Basic Psychology. University of Barcelona
9

10
11
12 **Correspondence to:** Lluís Fuentemilla. Cognition and Brain Plasticity Unit. Institute of
13 Biomedicine Research of Bellvitge (IDIBELL). Dept. of Basic Psychology (Campus
14 Bellvitge). Feixa Llarga s/n, 08907, L'Hospitalet (Barcelona), Spain. Phone: +34
15 934021038. Fax: +34 4024268. Email: lluis.fuentemilla@gmail.com
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48

49 **ABSTRACT**

50 Because memory retrieval often requires overt responses, it is difficult to determine to
51 what extent forgetting occurs as a problem in explicit accessing of long-term memory
52 traces. In this study, we used eye-tracking measures in combination with a behavioural
53 task that favoured high forgetting rates to investigate the existence of memory traces
54 from long-term memory in spite of failure in accessing them consciously. In 2
55 experiments, participants were encouraged to encode a large set of sound-picture-
56 location associations. In a later test, sounds were presented and participants were
57 instructed to visually scan, before a verbal memory report, for the correct location of the
58 associated pictures in an empty screen. We found the reactivation of associated
59 memories by sound cues at test biased oculomotor behaviour towards locations
60 congruent with memory representations, even when participants failed to consciously
61 provide a memory report of it. These findings reveal the emergence of a memory-guided
62 behaviour that can be used to map internal representations of forgotten memories from
63 long-term memory.

64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97

98 **INTRODUCTION**

99 It is commonly agreed that forgetting can be characterized by an apparent loss of
100 information already encoded and stored in an individual's long-term memory (Decay
101 theory (Woodworth, 1938); Consolidation theory (Dudai, 2004)) or by a process in
102 which old memories are unable to be retrieved from memory storage (Interference
103 theory (Underwood, 1957); Retrieval failure theory (Tulving and Thomson, 1973)). Yet,
104 disentangling between these two is not trivial. Because retrieval often requires a
105 conscious response, it is difficult to determine whether the eventual inability to recollect
106 memory information does actually represent a complete or partial vanishing of it or
107 instead, it appears as a problem in accessing consciously the selective memory trace.
108 Thus, it is of significance to find sensitive measures of memory that could provide
109 indexes of the existence of memory traces independently of overt responses.

110 Recent studies in humans indicate that eye movements can reveal memory for elements
111 of previous experience, even without appealing to verbal reports and without requiring
112 conscious recollection (Hannula et al., 2010). These effects rest on the observation that
113 eye movements are biased towards concurrent visual input matching or mismatching the
114 information encoded in past episodes (Hannula and Ranganath, 2009; Hannula et al.,
115 2009; Ryan et al., 2000; Ryan et al., 2007). However, because these experimental
116 settings are characterized by an at least partial display of visual information during
117 memory testing, the question of whether and to what extent any effects in eye
118 movement behavior are purely guided by internal memory representation (Ferreira et
119 al., 2008), by externally-guided visual stimulation triggering memory reactivation
120 (Richardson et al., 2009) or both, in the absence of awareness remains elusive.

121 To address questions about whether or not gaze is attracted to locations (i.e., indexing a
122 spatial memory trace) that had previously been occupied by studied content when blank
123 screens were presented at test, Spivey and colleagues studied eye movement patterns
124 when participants visually scan a blank screen while a memory cue is provided. Indeed,
125 participants' encoding of spatial information was revealed by their looking
126 behavior when answering a question that related to information that had previously
127 been presented in an empty region of space (Spivey and Geng, 2001; Richardson and
128 Spivey, 2000). These experiments showed that even in front of a completely blank grid,
129 participants would make systematic saccades to the region of space where they
130 perceived the event. This suggests that there might be an aspect of memory below the
131 level of explicit awareness that could be dissociated from retrieval operations. However,
132 these experimental findings were accounted for in circumstances in which memory for
133 spatial location was not tested directly (via explicit report), and therefore do not address
134 questions about whether or not memory for location was evident in eye movement
135 behavior absent explicit awareness. Thus, this methodological aspect hampered the
136 possibility to know whether eye movement behavior represents a sensitive measure of
137 memory that could provide indexes of the existence of memory traces independently of
138 overt responses.

139 In the current study, we sought to overcome these limitations with the use of eye-
140 tracking measures in combination with a new experimental approach. We designed a
141 behavioral task in which unique sound-picture-location associations were presented
142 once during an encoding phase. Critically, we set a large amount of associations during
143 encoding in order to impoverish their conscious recollection in a later memory test, thus
144 resembling conditions of severe memory forgetting, accompanying for instance certain

145 type of clinical and neurological population (i.e., patients with brain lesions in the
146 medial temporal lobe). At test, each sound was presented briefly and participants were
147 instructed to visually search in the empty scan for the correct location of the associated
148 picture (see Figure 1). Each trial finished with a verbal report whether or not they
149 remembered the location (Experiment 1) and a confidence judgment about the memory
150 for the object location (Experiment 2). Drawing on the idea that oculomotor behaviour
151 represents a reliable index of memory access of long-term memory, we expect that
152 sound cues at test would trigger a memory reactivation of the associated visual
153 information that could emerge as a biased pattern of eye movement towards space
154 locations congruent with memory trace representation, even for those trials in which
155 participants failed to consciously provide a memory report of it.

156
157

158 **MATERIAL AND METHODS**

159 **Ethics statement**

160 All participants provided written informed consent at the beginning of the experiment,
161 and were provided with a written debrief form after the experiment. All procedures were
162 approved by the local ethics committee (University of Barcelona). All participants were
163 compensated with credit courses for their participation.

164 **Experiment 1**

165 *Participants*

166 Twenty participants (12 women, $M = 20.2$ years, $SD = 1.1$) took part in Experiment 1.
167 All participants were students from the University of Barcelona. Four of them were
168 excluded from the analysis because of technical problems with eye movement
169 recording. Participants were with no history of neurological or psychiatric episodes, and
170 had normal visual acuity.

171 *Stimuli*

172 Stimuli consisted of 44 not semantically-related pairs of pictures and sounds that were
173 randomly selected for each participant. Pictures were black-and-white line drawings,
174 selected from a drawing database executed according to a set of rules that provide
175 consistency of pictorial representation (Snodgrass and Vanderwart, 1980). The pictures
176 have been standardized on four variables of central relevance to memory and cognitive
177 processing: name agreement, image agreement, familiarity, and visual complexity. All
178 44 auditory cues were natural sounds extracted from a database provided by the Spanish
179 Ministry of Education, Culture and Sports
180 (<http://recursostic.educacion.es/bancoimagenes/web/>). The sounds were all easily
181 recognizable (based on a pilot study with healthy participants; $n = 6$) and had a duration
182 ranging from 1 to 2 sec.

183 *Behavioural task*

184 The paradigm consisted in an encoding and a test phase (see Figure 1). During the
185 encoding phase, we encouraged participants to learn 44 different associations of sounds
186 cueing pictures, each appearing in a specific square of the screen (the 2 initial and the 2

187 last associations of the list served as primacy and recency effect buffers, and were not
188 examined at test). Pictures were equally distributed in the four possible locations and
189 presented randomly and counterbalanced for each participant. Participants were
190 informed before the encoding phase that each picture-sound-location was presented only
191 once and that a test would follow and that they would be required to indicate whether
192 they remembered the location and the picture. At encoding, a fixation cross remained in
193 the centre of the screen until eye fixation. A sound cue was presented with four empty
194 squares at the screen. At the end of the sound cue, a picture appeared in one of the
195 squares during 3 seconds. A complete empty screen of 2.5-3.5 seconds duration
196 separated the start of the next trial (i.e., indicated by the appearance of the fixation
197 cross). At test, each sound cue was presented and participants were asked, during a
198 subsequent ‘search period’ of 4 seconds, to fixate their viewing to the quadrant in which
199 picture appeared at encoding. In case they could not retrieve the picture location, they
200 were told to visually scan the monitor as if they were searching for the correct picture
201 location. They were told that such searching behaviour could be helpful to retrieve the
202 memory information. First, participants answered with ‘yes or no’ their recollection of
203 the picture location and then whether they could retrieve the picture itself. In such case,
204 they were further asked to name the picture object. To minimize as much as possible
205 any verbal representation of picture location (e.g. labelling upper-left corner as ‘one’,
206 upper-right corner as ‘two’ and so on), participants were not further asked to report it.
207 Once participant reported the verbal response, the experimenter manually (i.e., by
208 pressing the space bar) initiated the start of the next trial). The order of the trial
209 appearance was randomized during the both the study phase and the test phase.

210 *Procedure*

211 Stimuli were displayed on a black background on a 21” CRT monitor (1024 x 768
212 pixels, refresh rate 150Hz) with approximately 9 degrees of visual angle, corresponding
213 to square images of 9.5 cm at a viewing distance, using the Psychophysics toolbox
214 extensions for Matlab (www.psychtoolbox.org). The participants were seated with their
215 eyes approximately 60 cm from the computer screen with powerful speakers in a dimly
216 illuminated testing room.

217 Eye position was monitored at 500 Hz using an EyeLink II head-mounted eye tracker
218 (SR Research). Oculomotor data were parsed into saccades and fixations using
219 EyeLink’s standard parser configuration, which classifies an eye movement as a saccade
220 when it exceeds 30°/sec velocity or 8.000°/sec² acceleration and amplitude of gaze shift
221 was a minimum of 0.15°. The endpoints of saccades were determined with respect to
222 whether they fell within any of the four quadrant of stimulus presented on the screen.

223 Oculomotor memory-guided behaviour was indexed by the fixation (the relative number
224 of fixations) and the dwell time proportion (the relative time during which the gaze
225 remains fixated) on the correct square during the search period. This analysis was
226 performed using customized Matlab code (The Mathworks, Inc., Natick, MA) for each
227 trial and then results were sorted as those followed by a verbal report of having
228 remembered the location (recollected trials) or not (forgotten trials), independently of
229 whether picture labels could be verbally retrieved.

230

231 From a purely random behavior it would be expected the average proportion of eye
232 movement measures to each location follow a binomial distribution with $p = 0.25$.
233 Given that the number of trials is large, the binomial distribution can be approximated

234 with a normal distribution of mean 25%. Measures significantly over this value in
235 Student *t*-test were considered as evidencing the reactivation of memory representations
236 of picture location. Statistical significance in all the tests was set at $p < 0.05$, one-tailed.
237 Significant threshold was adjusted with Bonferroni correction for multiple comparisons
238 when more than 2 comparisons were made with the same measure. Measures of effects
239 size (Cohen's *d* or *f*) were also provided. SPSS (SPSS Inc., Chicago, USA) software
240 was used for the statistical analysis.
241

242 **Results**

243 Overall, the proportion of trials by which participants reported correctly the picture
244 label ($M = 24.7\%$, $SD = 17$) or indicated they had successfully retrieved the target
245 location (i.e., a 'yes' response) ($M = 36.7\%$, $SD = 17.6\%$) was very low (Figure 2A). As
246 expected though for both conscious recollection of picture and location, participants'
247 visual movements were strongly, albeit not exclusively, distributed in the correct square
248 location (fixation proportion: $M = 70.1\%$, $SD = 23.8\%$; dwell proportion: $M = 72.5\%$,
249 $SD = 18.4\%$). The possibility that participants' needed some time to fully recover
250 consciously the correct memory during the delay period may partially explain why the
251 pattern of eye movements was not distributed 100% in the correct location in those
252 cases. Another possibility is that the inherent exploratory behaviour of eye movements
253 induced shifts of eye movements throughout the screen during such long time period.

254 However, a disproportionate eye movement pattern towards the correct location was
255 also shown during the search period in those trials whose position participants explicitly
256 reported to have forgotten, independently of whether the object recall was correct or not
257 (Mean fixation proportion = 30.02% , $SD = 6.1\%$, $t(15) = 3.3$, $p < 0.001$, $d = 1.2$; Mean
258 dwell time = 30.5% , $SD = 5.7\%$, $t(15) = 3.8$, $p < 0.001$, $d = 1.4$). Importantly, these
259 results were consistent even when excluding from the analysis those trials that
260 participants were able to label verbally the picture object but not its location (Mean
261 fixation proportion = 28.9% , $SD = 7.1\%$, $t(15) = 2.15$, $p = 0.01$, $d = 0.8$; Mean dwell
262 time = 29.4% , $SD = 7\%$, $t(15) = 2.48$, $p < 0.01$, $d = 0.9$) (Figure 2B).

263
264

265 **Experiment 2**

266 The aim of experiment 2 was to address the question of whether the awareness test in
267 experiment 1 based on a 'Yes/No' answer could be insufficiently sensitive to failures in
268 memory access. Thus, it could be argued that on a subset of the trials participants felt
269 that they may know the location, but were not confident enough to indicate that they
270 had successfully recalled it. If this were the case, then viewing effects reported in
271 experiment 1 when explicit recall had 'failed' may actually reflect conscious access to
272 information about sound-location associations.

273 **Participants**

274 A new sample of 20 participants (17 women, $M = 23$ years, $SD = 4$) took part in
275 Experiment 2. All participants were students from the University of Barcelona.
276 Participants had no history of neurological or psychiatric episodes, and had normal
277 visual acuity.

278 **Procedure**

279 The same stimuli, apparatus and behavioural task as in experiment 1 were used, except
280 that participants were instructed to provide their confidence about the memory of the
281 location at the end of each trial during the recognition phase. Thus, just after the 'search
282 period' a message appeared on the screen requesting the participants to report whether
283 their memory for the location of the picture in such trial was '100% forgotten // 50%
284 forgotten // 50% remembered // 100% remembered'. In this way, we were allowed to
285 analyse separately those trials in which participants reported to be completely sure they
286 have forgotten the picture location (100% forgotten) and those trials that despite
287 participants had no access to picture location they could have some sort of feeling of
288 familiarity about which could be the location of the picture (50% forgotten). These
289 options were differentiated from those in which participants claimed that picture
290 location was poorly accessible (50% remembered) but they had the feeling they may do
291 a good job if they had to select between only two options (instead of the 4 possible
292 locations) and those trials in which participants actually remembered the picture
293 location (100% remembered).

294 **Data analysis**

295 Data analysis was the same as in experiment 1 except that fixation and dwell time
296 proportion on the correct square during the search period was analysed according to
297 participants' confidence judgment of having remembered the picture location.

298 **Results**

299 As in the previous experiment, in most cases during the test phase participants did not
300 recall the picture object (M = 80.2%, SD = 8.7%, with correct picture recall: M =
301 10.5%, SD = 6.9%; and with an erroneous object labelling: M = 9.2%, SD = 8.9%). For
302 these trials in which participants did not recall the picture object, the confidence level of
303 the memories for the object position was very low (M = 51.7%, SE = 4.6%; 100%
304 forgotten; M = 26.6%, SE = 3.2%; 50% forgotten; M = 21.7%, SE = 4.14%; 50%-100%
305 remembered) (Figure 3A).

306 Consistent with previous results, even when participants failed to consciously provide a
307 memory report of it, we observe a significant eye fixation pattern towards the correct
308 target location during the search period (100% forgotten condition: Mean Fixation
309 proportion for the target location M = 27.08% SD = 4.5%, $t(19) = 2.05$, $p < 0.05$, $d =$
310 0.66; Mean Dwell Time M=26.3% SD = 4.5%, $t(19) = 1.31$, $p = 0.1$; 50% forgotten
311 condition: Mean Fixation proportion for the target location M = 29.23% SD = 6.1%,
312 $t(19) = 3.1$, $p < 0.01$, $d = 1.1$; Mean Dwell Time M = 29.2 SD = 6.1, $t(19) = 3.1$, $p <$
313 0.01, $d = 1.01$). This is, when participants explicitly report to forget the location of the
314 object (100% and 50% forgotten conditions) eye movements (especially proportion of
315 fixations) showed a significant pattern towards the correct location. The lesser
316 sensitivity of Dwell Time measures to detect patterns of memory reactivation in the
317 100% forgotten condition could be partially explained because it has been shown that
318 search efficiency, or the overall time needed to find the target, is much more closely
319 correlated with the number of fixations than to dwell times (Zelinsky, 1996; Zelinsky
320 and Sheinberg, 1997).

321 Additionally, a repeated measure analysis (ANOVA) of eye movement patterns for the
322 target location at each confidence was calculated. Two participants were removed from
323 the 50%-100% remembered condition because they did not present responses at this
324 confidence level. This ANOVA yielded a main effect of confidence (Mean proportion
325 of fixations, $F(2,34) = 32.7, p < 0.001, f = 1.4$; Mean Dwell time, $F(2,34) = 34.8, p <$
326 $0.001, f = 1.4$). Interestingly, this effect showed both a significant linear (Proportion of
327 fixation, $F(1,17) = 81.9, p < 0.001, f = 2.2$; Dwell Time, $F(1,17) = 82.3, p < 0.001, f =$
328 2.2) and a quadratic (Proportion of fixation, $F(1,17) = 6.68, p = 0.019, f = 0.6$; Dwell
329 Time, $F(1,17) = 5.9, p = 0.026, f = 0.6$) trend, thereby suggesting that differences
330 between confidence levels may not be totally proportional across them. In fact, a paired
331 Student *t*-tests (two-tail) comparing the different confidence levels confirmed
332 significant differences (after correction for multiple comparisons, only p-values under
333 0.016 can be considered statistically significant) between the remembered and the
334 forgotten conditions for the eye movement pattern (100% forgotten vs. 50%-100%
335 remembered Mean proportion of fixation ($t(17) = -9.06, p < 0.001, d = -3.1$), Mean
336 Dwell time ($t(17) = -9.07, p < 0.001, d = -3.1$); 50% forgotten vs. 50%-100%
337 remembered: Mean proportion of fixation ($t(17) = -6.7, p < 0.001, d = -2.3$), Mean
338 Dwell time ($t(17) = -6.8, p < 0.001, d = -2.3$), see Figure 3B). However, there were no
339 significant differences within the 100% and the 50% forgotten condition (Proportion of
340 fixation, $t(17) = 1.01, p = 0.33, d = 0.34$; Dwell Time, $t(17) = 1.36, p = 0.19, d = 0.47$),
341 thereby excluding the possibility that the observed towards the target location can be
342 interpreted only as differences in confidence level.

343

344 Finally, in order to rule out the possibility that the observed memory-guided eye
345 movement patterns could be explained as a bias to eye movement preferences to
346 specific locations, we tested whether target positions were equally distributed across the
347 four positions for each condition in our participant's performance. A one-factor (4
348 quadrant position) ANOVA indicated that the proportion of recalled location did not
349 differ among the quadrants for any of the confidence conditions ('100% forgotten':
350 $F(3,57)=1.9, p=0.14, f=0.32$; '50% forgotten' : $F(3,57)=1.7, p=0.18; f=0.3$; '50%-100%
351 remembered': $F(3,57)=1.7, p=0.17, f=0.3$), thereby discarding a bias in eye movement
352 patterns for a preferred location.

353

354

355 **DISCUSSION**

356 In this study we used eye-tracking measures in combination with a new experimental
357 approach to test the idea that oculomotor behaviour may represent a reliable index of the
358 existence of memory traces from long-term memory in spite of failure in accessing them
359 consciously. Our findings show that the reactivation of associated memories by sound
360 cues at test biased oculomotor behaviour towards locations congruent with memory
361 representations, even when participants failed to consciously provide a memory report
362 of it.

363 Past studies have emphasized the implicit nature of eye movement patterns in
364 recognition memory tests. Eye movements have been found to reflect previous exposure
365 even in the absence of explicit awareness of the change (Hannula and Ranganath, 2009;
366 Althoff and Cohen, 1999), and regardless of whether the task required intentional
367 retrieval (Hannula et al., 2007). In fact, differential viewing of studied stimuli can be
368 observed well in advance of explicit identification of that stimulus (Hannula et al.,

369 2012). The present study is consistent with these past results in suggesting that eye
370 movements provide an important sensitive measure of memory and expand them by
371 showing that eye movement patterns are even biased towards memory content when this
372 is reactivated by a non-visual associative cue.

373 Current and previous research provides experimental evidence that memory functioning
374 can be tested reliably with the study of eye movements without the need to rely on
375 conscious responses. Thus, patterns of eye movement varied according to the degree of
376 how visual information matches/mismatches with existent long-term memory traces
377 (Hannula and Ranganath, 2009; Ryan et al., 2000; Smith et al., 2000). Our findings add
378 valuable information in tightening even more this link in indicating that, in fact, eye
379 movement behaviour can be guided by the internal memory representation without any
380 concurrent input to the visual system. In experiment 2, we further found that such
381 memory-guided pattern of eye movements took place even in those cases in which
382 participants reported confidently the information had vanished from long-term memory,
383 thereby suggesting that eye movement behaviour may act, at least partially,
384 independently of subjective confidence of memory trace existence.

385 [Despite that the current experimental design exploited the advantages of eye movement](#)
386 [measuring to study implicit traces of memory content, others have shown that memory](#)
387 [performance could be affected, for instance, by the pattern of eye movements preceding](#)
388 [a recognition task \(Christman et al., 2003\). These findings are in line with successful](#)
389 [episodic encoding of neurophysiological data into long-term memory \(Guderian et al.,](#)
390 [2009\) and successful episodic memory retrieval \(Addante et al., 2011\), and are](#)
391 [modulated by preceding brain states of activity reflected as changes in the ongoing](#)
392 [oscillatory activity at the theta range \(4-8Hz\). The extent to whether eye movements and](#)
393 [theta activity could be functionally related remains unknown. Therefore, the](#)
394 [combination of measuring eye movement patterns preceding and during a memory task](#)
395 [may offer new venues to study the mechanisms and the specific memory content](#)
396 [underlying process of both memory success and memory failure.](#)

397 The possibility to explore reminiscences of memory traces despite participants' inability
398 to subjectively evaluate the quality or the accessibility of the long-term memories can
399 be seen as an important hallmark in creating new approaches to explore memory
400 functioning ahead of participants' explicit report or other overt responses. However,
401 some methodological limitations may require further investigation in future
402 experimentation. For instance, even though our findings hold for those trials in which
403 the participant declared not being aware of any type of information related to the
404 memory event (i.e., picture imagery and space location), it is still possible that our
405 design cannot always distinguish information loss from impaired access as a source of
406 forgetting. Thus, it could well be the case that other standard memory tests, e.g.
407 recognition tasks, could enhance the participants' ability to access memories from long-
408 term through explicit responses. Methodological aspects as such call for further
409 experimentation in the future.

410 At a broader level, current findings lend support to the notion that the putative systemic
411 division of labour between conscious and unconscious memory is not so clean (Hannula
412 and Greene, 2012). For instance, Voss and Paller (2010) suggested that the relationship
413 between recognition performance and explicit memory might not be so straightforward.
414 Indeed, changes in strategy, based for example on encouragement to guess, can improve
415 recognition performance, but these performance improvements do not always reflect

416 conscious retrieval processes (Voss and Paller, 2010; Voss et al., 2008; Voss and Paller,
417 2009). Another example can be seen in the change blindness effect. This effect
418 documents the situation in which the memory representation of scene information and
419 conscious awareness of perceptual changes may not go always together (Simons et al.,
420 2002). In these experiments, participants are unable to consciously detect changes
421 between two scene presentations, although these experiments also show that people
422 often do have a representation of some aspects of the pre-change scene even when they
423 fail to report the change (Simons et al., 2002). Present results contributed to the growing
424 evidence that long-term memory traces can be accessed implicitly. And, in doing so,
425 they challenge the view by which memory systems are essentially divided as to whether
426 they support conscious access to remembered content or not.

427 In sum, the current results reveal the emergence of a memory-guided behaviour that can
428 be used to unconsciously map internal representations of associative memories from
429 long-term memory. They may provide a valuable tool that could open the door to the
430 exploration of, for instance, neurological patients with severe impairments in memory
431 recall and allow the use of comparable paradigms in animals and humans. Future work
432 may put an effort in creating behavioural tasks that could reliably identify memory
433 traces at individual level. While we wait for such advance, they reveal the possibility of
434 investigating memory content reactivation even when explicit (conscious) recollection
435 has failed.

436
437
438

439 **Acknowledgments.** The authors thank Maria Solé, Laura Pérez and Juan Manuel
440 García for their assistance in conducting this study. L.F. is a fellow of the Ramon y
441 Cajal program. This research study was supported by grants from the Spanish
442 Government (PSI2010-15024 to L.F). The authors declare no competing financial
443 interests.

444
445
446
447

448 REFERENCES

449 [Addante RJ, Watrous AJ, Yonelinas AP, Ekstrom AD, Ranganath C \(2011\). Prestimulus](#)
450 [theta activity predicts correct source memory retrieval. *Proc Natl Acad Sci USA* 108,](#)
451 [10702-10707](#)

452

453 Althoff RR, Cohen NJ (1999). Eye-movement-based memory effect: A reprocessing
454 effect in face perception. *Journal of Experimental Psychology: Learning, Memory, and*
455 *Cognition* 25:1-14

456

457 [Christman SD, Garvey KJ, Propper RE, Phaneuf KA \(2003\). Bilateral eye movements](#)
458 [enhance the retrieval of episodic memories. *Neuropsychology* 17: 221-22](#)

459

460 Dudai Y (2004). The neurobiology of consolidations, or, how stable is the engram?
461 *Annual Review in Psychology* 55: 51-86.

462

463 Ferreira F, Apel J, Henderson JM (2008) Taking a new look at looking at nothing.
464 *Trends in Cognitive Science* 11: 405-410.

465
466 Guderian S, Schott BH, Richardson-Klavehn A, Düzel E (2009) Medial temporal theta
467 state before an event predicts episodic encoding success in humans. *Proc Natl Acad Sci*
468 *USA* 106: 5365-5370.
469
470 Hannula DE, Ryan JD, Tranel D, Cohen NJ (2007). Rapid onset relational memory
471 effects are evident in eye movement behavior, but not in hippocampal amnesia. *J Cogn*
472 *Neurosci* 19: 1690-705
473
474 Hannula DE, Althoff RR, Warren DE, Riggs L, Cohen NJ, Ryan JD (2010). Worth a
475 glance: using eye movements to investigate the cognitive neuroscience of memory.
476 *Frontiers in Human Neuroscience* 8: 4-166.
477
478 Hannula D E, Ranganath C (2009). The eyes have it: hippocampal activity predicts
479 expression of memory in eye movements. *Neuron* 63: 592-599.
480
481 Hannula DE, Baym CL, Warren DE, Cohen NJ (2012). The eyes know: eye movements
482 as a veridical index of memory. *Psychol Sci* 23: 278-287.
483
484 Richardson DC, Altmann GT, Spivey MJ, Hoover MA (2009). Much ado about eye
485 movements to nothing: a response to Ferreira et al.: taking a new look at looking at
486 nothing. *Trends in Cognitive Science* 13: 235-236
487
488 Richardson DC, Spivey MJ (2000). Representation, space and Hollywood Squares:
489 looking at things that aren't there anymore. *Cognition* 76: 269-95.
490
491 Ryan JD, Althoff RR, Whitlow S, Cohen NJ (2000). Amnesia is a deficit in relational
492 memory. *Psychol Sci* 11: 454-461
493
494 Ryan JD, Hannula DE, Cohen NJ (2007). The obligatory effects of memory on eye
495 movements. *Memory* 15:508-525
496
497 Simons DJ, Chabris CF, Schnur T, Levin DT (2002). Evidence for preserved
498 representations in change blindness. *Conscious Cogn* 11: 78-97.
499
500 Smith CN, Hopkins RO, Squire LR (2006). Experience-dependent eye movements,
501 awareness, and hippocampus-dependent memory. *J Neurosc* 26: 11304-11312
502
503 Snodgrass JG, Vanderwart M (1980). A standardized set of 260 pictures: norms for
504 name agreement, image agreement, familiarity, and visual complexity. *J Exp Psychol*
505 *Hum Learn* 6: 174-215
506
507 Spivey MJ, Geng JJ (2001). Oculomotor mechanisms activated by imagery and
508 memory: eye movements to absent objects. *Psychol Res* 65: 235-41.
509
510 Tulving E, Thomson DM (1973). Encoding specificity and retrieval processes in
511 episodic memory. *Psychol Rev* 80: 352-373
512
513 Underwood BJ (1957). Interference and forgetting. *Psychol Rev* 64: 49-60
514

515 Voss JL, Baym CL, Paller KA (2008). Accurate forced-choice recognition without
516 awareness of memory retrieval. *Learn Mem* 15: 454-9
517
518 Voss JL, Paller KA (2009). Recognition without awareness in humans and its
519 implications for animal models of episodic memory. *Commun Integr Biol* 2: 203-4.
520
521 Voss JL, Paller KA (2010). What makes recognition without awareness appear to be
522 elusive? Strategic factors that influence the accuracy of guesses. *Learn Mem* 17:460-8.
523
524 Woodworth RS (1938). *Experimental Psychology*, Holt, Rinehart & Winston, Inc., New
525 York.
526
527 Zelinsky GJ (1996). Using eye saccades to assess the selectivity of search movements.
528 *Vision Res.* 36: 2177-87.
529
530 Zelinsky GJ, Sheinberg DL (1997) Eye movements during parallel-serial visual search.
531 *J Exp Psychol Hum Percept Perform.* 23: 244-262.
532
533
534

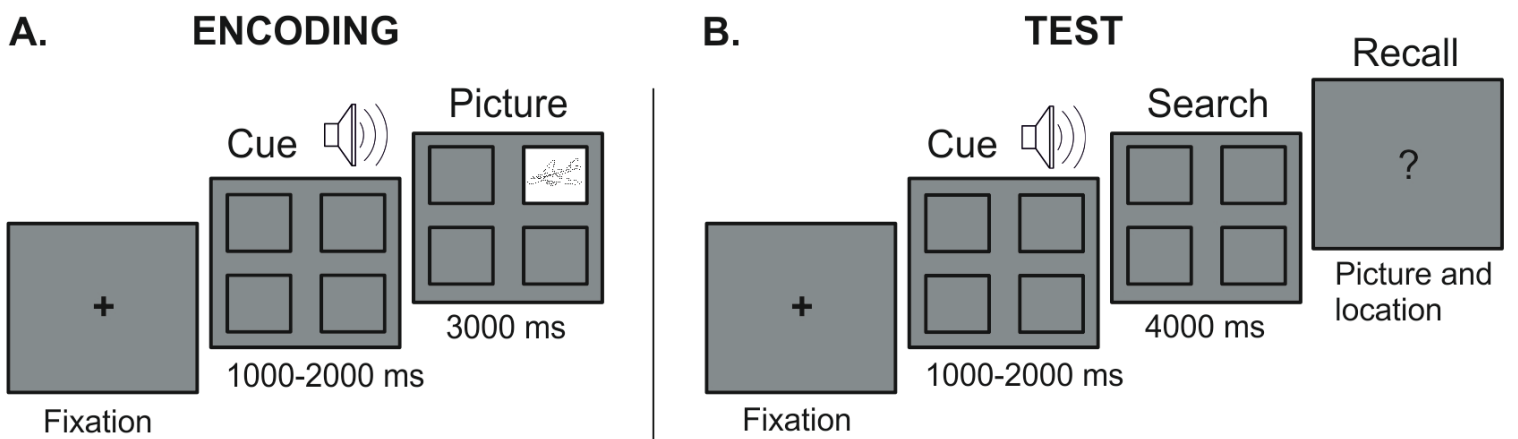
535 **FIGURE LEGENDS**

536 **Figure 1. Experimental Design.** At encoding **(A)**, a fixation cross remained in the
537 centre of the screen until eye fixation. A sound cue was presented with four empty
538 squares at the screen. At the end of the sound cue, a picture appeared in one of the
539 squares during **3 seconds**. A complete empty screen of **2.5-3.5 seconds** duration
540 separated the start of the next trial. At test **(B)**, after a fixation cross, each sound cue was
541 presented with the four empty squares on the screen. At the end of the sound cue, the
542 searching period started. Participants were instructed thereafter to verbally report the
543 associated picture or to indicate ‘no memory’ when the information was forgotten.

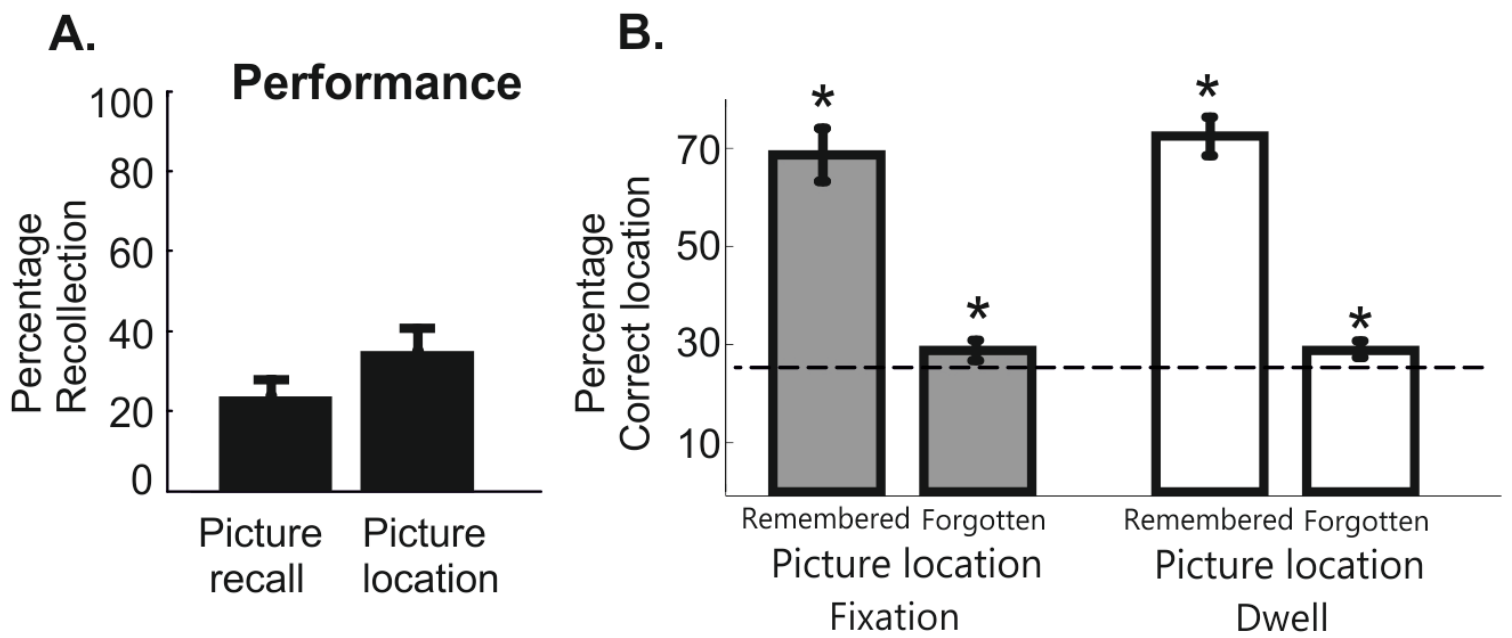
544 **Figure 2. Behavioral data in experiment 1.** **(A)** Percentage of correct picture and
545 location recall responses averaged across participants for Experiment 1. **(B)** Bar plots
546 represent the proportion of fixation and dwell time in the correct picture location
547 averaged across participants in Experiment 1. Error bars denote Standard Error of the
548 Mean. *, $p < 0.05$; ‘n.s.’ denotes $p > 0.05$.
549

550 **Figure 3. Behavioral data in experiment 2.** **(A)** Percentage behavioural responses
551 averaged across participants for Experiment 2. **(B)** Bar plots represent the proportion of
552 fixation and dwell time in the correct picture location averaged across participants in
553 Experiment 2. Error bars denote Standard Error of the Mean. *, $p < 0.05$; ‘n.s.’ denotes
554 $p > 0.05$.
555

Figure 1.JPEG



Experiment 1



Experiment 2

