Neurophysiological and computational mechanisms of non-associative and associative memories during complex human behavior

Yuchen Xiao[1,2*], Paula Sánchez López[3,4*], Ruijie Wu[5,6*], Ravi Srinivasan[7], Peng-Hu Wei[8,9], Yong-Zhi Shan[8,9], Daniel Weisholtz[10], Garth Rees Cosgrove[10], Joseph R Madsen[11], Scellig Stone[11], Guo-Guang Zhao[8,9‡], Gabriel Kreiman[11,12‡]

[1]Harvard University, Cambridge, MA, USA

[2]Westlake University, Hangzhou, Zhejiang, China

[3]Ecole Polytechnique Fédérale de Lausanne, Lausanne, Switzerland

[4]Harvard Medical School, Boston, MA, USA

[5]State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing, China

[6]Hefei Comprehensive National Science Center, Institute of Artificial Intelligence, Hefei, China

[7]Eidgenössische Technische Hochschule (ETH), Zurich, Switzerland.

[8]Department of Neurosurgery, Xuanwu Hospital, Capital Medical University, Beijing, China

[9]National Center for Neurological Disorders, Beijing, China

[10]Brigham and Women's Hospital, Harvard Medical School, Boston, MA, USA

[11]Boston Children's Hospital, Harvard Medical School, Boston, MA, USA

[12]Center for Brains, Minds and Machines, Cambridge, MA, USA

*These authors contributed equally to this work.

[‡]To whom correspondence should be addressed: Gabriel.kreiman@tch.harvard.edu

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Abstract

The ability to transiently remember what happened where and when is a cornerstone of cognitive function. Forming and recalling working memories depends on detecting novelty, building associations to prior knowledge, and dynamically retrieving context-relevant information. Previous studies have scrutinized the neural machinery for individual components of recognition or associative memory under laboratory conditions, such as recalling elements from arbitrary lists of words or pictures. In this study, we implemented a well-known card-matching game that integrates multiple components of memory formation together in a naturalistic setting to investigate the dynamic neural processes underlying complex natural human memory. We recorded intracranial field potentials from 1,750 depth or subdural electrodes implanted in 20 patients with pharmacologically-intractable epilepsy while they were performing the task. We leveraged generalized linear models to simultaneously assess the relative contribution of neural responses to distinct task components. Neural activity in the gamma frequency band signaled novelty and graded degrees of familiarity, represented the strength and outcome of associative recall, and finally reflected visual feedback on a trial-by-trial basis. We introduce an attractor-based neural network model that provides a plausible first-order approximation to capture the behavioral and neurophysiological observations. The large-scale data and models enable dissociating and at the same time dynamically tracing the different cognitive components during fast, complex, and natural human memory behaviors.

Introduction

Working memory serves as a fundamental component of our cognitive abilities, enabling us to store and retrieve immediate information. In stark contrast to most efforts in current artificial intelligence algorithms, the transient storage of memories occurs in a largely unsupervised fashion, with single or limited exposure. The formation and recall of memories require assessing novelty versus familiarity, building bridges between sensory inputs and prior knowledge, connecting spatial and temporal cues and effectively retrieving information in the context of current task demands. While substantial literature exists on neural responses in laboratory-based tasks for separate components of working memory, our understanding of how these components are integrated and coordinated in real-life tasks remains limited.

Non-associative recognition memory refers to the ability to judge the prior occurrence of a stimulus. Judging whether an item is novel or not is necessary for its successful memory encoding[1], and recognizing an item as familiar facilitates memory retrieval[2]. Several studies have documented correlates of recognition memory for novelty versus familiarity, primarily but not exclusively, in medial temporal lobe (MTL) structures in rodents, monkeys, and humans[3-14]. Many studies have focused on tasks that involve presenting a list of items, such as words, pictures, or video clips, and either recalling items from these lists or assessing recognition memory for those items (e.g.,[6,8-12,15-20]). Both novel and familiar items need to be incorporated into the body of prior knowledge by forming novel associations. Associative memory refers to the ability to link items or evaluate the correctness of such associations (e.g.,[21-30]). Associative memory has been commonly investigated by having participants learn pairs of items and recalling one of the two items given the other or assessing whether a given association is correct or not.

Although recognition memory and associative memory have been largely studied separately, they are not independent in real-world memory tasks. The successful implementation of associative memory is contingent on basic recognition processes. To understand the connections and dissociations between different components of memory formation during natural and complex behavior, here we recorded intracranial field potentials from 20 patients with pharmacologically intractable epilepsy while they played a classical card matching game,

colloquially known as the "Memory" game (**Figure 1, Movie S1**). We focused on the neural activity in the gamma frequency band (30-150 Hz)[31-35]. Participants thrived in the task, demonstrating dependence on the task memory demands and temporal recency effects. Using generalized linear models, we characterized how neural responses are modulated by the different behavioral components involved in the task. Our results demonstrate that neural circuits can represent novelty and familiarity independently of the sensory content, along with the strength and outcome of associative recall on a trial-by-trial basis.

To better understand the mechanisms underlying memory formation and retrieval, we turn to computational models[36]. Models rooted in persistent neuronal activity[37-45] provide important insights into working memory's neural basis. Recent perspectives, including those involving attractor networks[46-52], have also highlighted the significance of Hebbian synaptic plasticity and short-term depression and facilitation as means to enhance memory encoding[53-57]. As a proof-of-principle, we introduce a simple attractor-based neural network model that provides a first-order approximation to describe the behavioral and neurophysiological observations.

Results

We recorded intracranial field potentials (IFPs) from 20 patients with pharmacologically intractable epilepsy implanted with depth electrodes (**Table S1**, one participant also had subdural surface electrodes). Participants played a memory-matching game (**Figure 1, Movie S1, Methods**). Each trial consisted of two self-paced clicks. Clicking on a tile revealed an image (**Figure 1A**). Image categories included person, animal, food, vehicle, and indoor scenes. If the two tiles in a trial contained the same image (*match*, **Figure 1B**), the two tiles turned green and could not be clicked again for the remainder of the block. If the two images were different (*mismatch*, **Figure 1A** and **1C**), the two tiles turned black and could be clicked again. Participants started in a 3×3 tile board block like the one shown in **Figure 1** and progressed to more difficult blocks (4×4, 5×5, 6×6, or 7×7 tiles). All tiles had a corresponding match, except for one tile in the boards with an odd number of tiles (3×3, 5×5, and 7×7).

Mismatch trials showed longer reaction times and were associated with less frequent and less recent exposure to matching pairs

The average number of clicks per tile increased with difficulty (board size), as expected (**Figure 2A**). All participants performed much better than a memoryless model (random clicking, $p<0.001$, here and in subsequent tests unless stated otherwise: permutation test, 5,000 iterations, one-tailed) and performed worse than a model assuming perfect memory ($p<0.001$, **Figure 2A**). The reaction time (RT) was defined as the time interval between the first and second clicks within a trial (**Figure 1A**). The reaction time was longer for mismatch than match trials for all board sizes ($p<0.007$, **Figure 2B**).

For a tile in a given trial, we defined *n-since-last-click* (nslc) as the number of clicks elapsed since the last time *the same tile* was clicked (**Figure 1A**-**B**). As expected, nslc increased with board size ($p<0.001$, linear regression, F-test, **Figure 2C**-**D**). For the 2nd tile, nslc was larger in mismatch compared to match trials for all board sizes except the 3×3 case ($p<0.001$, **Figure 2D**), a reflection of the decay in memory for tiles that were not seen recently. The larger nslc in mismatch trials also held for the 1st tile only for the 7×7 board size ($p<0.001$, **Figure 2C**). If the participants believe that they know the locations of both tiles in a matching pair, a reasonable strategy is to click first the tile they are less sure about, likely because they have seen this tile earlier rather than later in the block. This strategy accounts for the differences between the 1st tile (**Figure 2C**) and 2nd tile (**Figure 2D**).

For a tile in a given trial, we defined *n-since-pair* (nsp) as the number of clicks since the last time when *its matching pair* was seen (**Figure 1A**, **C**). As expected, nsp increased with board size given the increased difficulty ($p<0.001$, linear regression, F-test, **Figure 2E-2F**). Additionally, the more recent the tile's matching pair was seen, the more likely the trial was a match. Thus, nsp was larger in mismatch compared to match trials in all cases except the 3x3 board size for the 1st tile ($p<0.001$, **Figure 2E**). For the 2nd tile, nsp for any match trial was always one because the matching pair would have been revealed in the previous click, by definition. Thus, there was a large difference between nsp between match and mismatch trials ($p<0.001$, **Figure 2F**).

We performed infrared eye-tracking on ten healthy participants while they performed the same task. Participants fixated on the tile they clicked, both for the first and second tiles, and both for match and mismatch trials (**Figure S1**). For the first tile, there was no difference in the dynamics of saccades towards and away from the target tile between match and mismatch trials (**Figure S1A**) after equalizing the RT and the distances between the 1st and the 2nd tiles. For the second tile, there was no difference in the dynamics of saccades toward the target tile before the click. However, within the 1 second window after the 2nd click, the distance to the center of the tile was, on average, 1.76 dva (degrees of visual angle) larger for match than mismatch trials (**Figure S1B**). This small difference may be attributed to participants' lingering slightly longer during mismatch trials, arguably in an effort to remember the tile.

Neural signals reflect novelty and familiarity

We recorded intracranial field potentials from 1,750 electrodes (**Table S2**). We excluded 582 electrodes due to bipolar referencing, locations in pathological sites, or signals containing artifacts (**Methods**). We included in the analyses 676 bipolarly referenced electrodes in the gray matter (**Figure S2**) and 492 in the white matter (**Figure S3**). **Table S2** describes electrode locations separated by brain region and hemisphere. Although the white matter is presumed to contain mostly myelinated axons, previous studies have shown that intracranial field potential signals from the white matter can demonstrate biologically meaningful information[58,59]. Such signals could reflect small errors in electrode localization on the order of ~2 millimeters and also the spread of intracranial field potential signals over 1 to 5 millimeters[32,33,60-62], implying that white matter electrodes may still capture activity from gray matter. Indeed, we show here that electrodes in the white matter reveal task-relevant properties and therefore included electrodes in the white matter in our analyses. To avoid confusion about the origin of the signals, we focused on the gray matter electrodes in the main text and reported results from electrodes in the white matter in the Supplementary Material. None of the conclusions in this study would change if we were to report the results from electrodes in the gray matter exclusively.

We built two generalized linear models (GLM) to characterize how the neural responses depended on the cognitive demands of each trial. The first model focused on the neural responses to the 1st tile, and the second model on the 2nd tile. In both cases, we focused on predicting the area under the curve (AUC) of the gamma band power (30-150 Hz) in each trial (**Methods**). For the first GLM, the time window started when the 1st tile was clicked and ended at a time corresponding to the 90th percentile of the distribution of reaction times (time difference between the 1st and the 2nd clicks, **Figure 1A**). This criterion was a reasonable tradeoff between minimizing overlap with responses after the 2nd tile and maximally capturing information before the 2nd tile. For the second model, the time window started with the 2nd click and ended one second afterward.

We considered 15 predictors for the GLM models, including whether a trial was a match or not, reaction time, n-since-last-click (nslc), and n-since-pair (nsp), the variables introduced in **Figures 1**-**2**. We also included additional predictors: first-click (whether a tile was clicked for the first time), n-times-seen (number of times an image had been seen), next-match (whether the subsequent trial was a match), board size, x and y position of the clicked tile within the board, distance between the first and the second tiles, and whether the image contained a person, animal, food, or vehicle. **Table 1** lists all the predictors and their definitions. Since several predictors were correlated with each other (**Figure S4A**-**B**), we computed the variance inflation factor (VIF)[63], a metric commonly used to account for correlations between predictors in generalized linear models. The VIF of each predictor was smaller than 3 for all participants (**Figure S4C**-**D**). Therefore, the correlations between predictors did not harm the performance of the models (**Methods**).

When the first tile in a trial was clicked, its status in memory guided the following actions. If it was a new image, the participant needed to encode it in memory for future retrieval. Thus, the ability to detect novelty is the first step for successful encoding. The predictor *first-click* described novelty and had a value of 1 whenever a tile was seen for the first time and 0 otherwise. If a tile had been viewed before, it would appear familiar to the participant, and the degree of familiarity depended on how long ago that tile had been seen last. The predictor n-since-last-click (**Figure 1A**-**B, Figure 2C**-**D**) captures the notion of familiarity; the smaller the nslc value, the more

196 familiar the tile is because that same tile was seen more recently and there were fewer
197 competing stimuli encountered in between.

198 **Figure 3A-D** shows the neural activity of an electrode located in the right lateral
199 orbitofrontal cortex (arrow in **Figure 3D**), whose responses to the first tile correlated with novelty.
200 The GLM analysis indicated that first-click was a significant predictor of the neural responses
201 (**Figure 3A**). The neural responses to the first tile showed a decrease in activity for novel tiles
202 compared to tiles that had been seen before (**Figure 3B**), which could also be readily seen in
203 individual trials (**Figure 3C**). This decrease in activity is reflected by the negative sign in the GLM
204 first-click predictor (**Figure 3A**).

205 Novelty was a significant predictor of the neural responses after the first tile ($p<0.01$, GLM)
206 for 50 electrodes in the gray matter (7.4% of the total, **Table S3A**, **Figure 3D**) and 33 electrodes
207 in the white matter (6.7% of the total, **Table S3B**). The lateral orbitofrontal (LOF) cortex and pars
208 opercularis contained significantly more electrodes than expected by chance ($p<0.01$, **Methods**).

209 **Figure 3E-H** shows the neural activity of an electrode located in the left pars opercularis
210 (arrow in **Figure 3H**), whose responses to the first tile correlated with familiarity. The GLM
211 analysis indicated that both n-since-last-click (nslc) and first-click were significant predictors of
212 the neural responses ($p<0.001$, GLM, **Figure 3E**). Novel tiles (completely unfamiliar tiles, **Figure**
213 **3F**, blue) elicited strong responses, followed by less familiar tiles (higher nslc, **Figure 3F**, yellow).
214 Familiar tiles (nslc=1, i.e., tiles that had just been seen in the preceding trial) elicited almost no
215 response (**Figure 3F**, red). The strong correlation between the neural responses, novelty, and
216 familiarity can also be readily appreciated in individual trials (**Figure 3G**).

217 The reaction time was also a significant predictor for the neural responses recorded from
218 this electrode (**Figure 3E**). However, the differences in neural responses signaling novelty and
219 distinct degrees of familiarity *cannot* be explained by differences in reaction time. The differences
220 in neural responses associated with novelty and familiarity persisted after reaction time
221 equalization (see vertical dashed lines indicating equalized RT in **Figure 3F**).

222 The nslc predictor was statistically significant ($p<0.01$, GLM) in 45 gray matter electrodes
223 (6.7% of the total, **Table S4A**, **Figure 3H**) and 32 white matter electrodes (6.5%, **Table S4B**, **Figure**
224 **S5D**). **Figure S5** shows an example electrode located in the white matter whose responses

225 correlated with novelty and familiarity. The majority of electrodes (82.2%) showed a positive
226 correlation between the neural responses and nslc as illustrated in **Figure 3E-G**. The remaining
227 electrodes (17.8%) showed a negative correlation, i.e., stronger neural responses for more
228 familiar items. **Figure S6** depicts an example electrode located in the right pars opercularis
229 showing a negative correlation between familiarity and neural responses.

230 Both the electrode in **Figure 3E-H** and the one in **Figure S6** revealed first-click as a
231 significant predictor in addition to nslc, meaning that their responses not only reflected the
232 familiarity gradient but also represented novelty. The electrodes that showed both first-click and
233 n-since-last-click as significant predictors (20 electrodes) are denoted by red circles in **Figure 3D**
234 and **Figure 3H**. Among these 20 electrodes, the signs of the t-statistic for the first-click and n-
235 since-last-click predictors were consistent for 18 electrodes (16 positive and 2 negative). Only
236 two electrodes exhibited opposite signs. These results indicate that novelty largely resembles
237 extremely low familiarity in terms of the underlying neural responses.

238

239 **Neural signals show anticipation of the trial's outcome**

240

241 After seeing the 1st tile, participants attempt to find the tile's pair. If the 1st tile's pair was
242 never encountered before, this is a random choice among the unseen tiles. If the tile's pair is
243 unfamiliar, recalling a match is error-prone and often leads to mismatches (**Figure 2E**). For highly
244 familiar cases, participants can retrieve the correct location to find the match tile. Therefore, we
245 asked whether the neural responses after exposure to the first tile and before seeing the 2nd tile
246 could predict successful retrieval.

247 **Figure 4** shows the neural activity of an electrode located in the right lateral orbitofrontal
248 cortex (arrow in **Figure 4E**), whose responses were predictive of successful retrieval. The GLM
249 analysis indicated that match was a significant predictor of the neural responses ($p<0.001$, **Figure**
250 **4A**). This electrode showed stronger responses during match trials (**Figure 4B**, green) than during
251 mismatch trials (**Figure 4B**, black). These differences can even be appreciated in single trials
252 (compare **Figure 4C** versus **Figure 4D**). Of note, these differences are evident shortly after
253 visualization of the first tile, with a peak at 500 ms after clicking the first tile, well before clicking

254 the second tile, when the participant did not know for certain yet whether the trial would be a
255 match or not. Thus, the strong neural differences between match and mismatch trials reflect the
256 participant's internal retrieval of the correct pairs' locations.

257 Whether a trial was a match or not was a significant predictor of the neural responses for
258 32 electrodes in the gray matter (4.7% of the total, **Table S5A**, **Figure 4E**) and 30 electrodes in
259 the white matter (6% of the total, **Table S5B**, **Figure S7**). For an example electrode in the white
260 matter see **Figure S7**. In most cases (91%), neural activity was higher during match trials than
261 during mismatch trials, as illustrated in **Figure 4**. The locations of all these electrodes, shown in
262 **Figure 4E** (gray matter) and **Figure S7** (white matter), reveal that the majority were located in the
263 lateral orbitofrontal (LOF) cortex, the medial temporal lobe, and the insula. The LOF cortex
264 contained significantly more electrodes than expected by chance ($p<0.01$, **Methods**).

265 The peak in neural activity occurred at approximately 500 ms after the 1st click (**Figure 4B**).
266 As discussed in the previous section, the match predictor correlated with several other predictors
267 (**Figure S4**). However, the GLM analysis shows that the match's presence, but not other
268 predictors, accounts for the neural responses (**Figure 4A**). To further establish this point, **Figure**
269 **S8A** shows the responses of this same electrode, in the same format as **Figure 4B**, after equalizing
270 the n-since-last-click (nslc) distributions for match and mismatch trials by subsampling the data.
271 The same conclusions hold in this case. Furthermore, **Figure S8B** shows each match trial's gamma
272 power AUC versus the value of n-since-last-click and **Figure S8C** displays the same data from
273 mismatch trials. The variable nslc did *not* account for the neural responses in either case ($p>0.18$,
274 linear regression). Similar conclusions hold for the other predictors.

275 **Figure S9** shows another example electrode located in the left middle temporal gyrus
276 where the match was a significant predictor for the gamma band activity between the 1st and 2nd
277 tiles. Similar to the LOF electrode in **Figure 4**, the gamma power during match trials was higher
278 than during mismatch trials. However, the pattern of modulation in this electrode was sustained
279 rather than transient (compare **Figure S9** versus **Figure 4B**-**D**). The change in gamma power was
280 also evident in individual trials (**Figure S9B**-**C**). These observations suggest that the middle
281 temporal and lateral orbitofrontal regions might be functionally distinct during memory retrieval.

In sum, these results indicate that even before the actual realization of whether a trial was a match or mismatch (i.e., before the onset of the 2nd tile), there were distinct neural responses that were predictive of the trial's outcome.

Neural signals reflect the strength of memory retrieval

In addition to reflecting the outcome of a given trial (match versus mismatch), we considered the *n-since-pair* (nsp) predictor as a proxy for the degree of confidence or strength of memory retrieval. The smaller the nsp, the more recently *the tile's pair* had been seen (**Figure 2E**-**F**). This predictor is different from n-since-last-click, which indicates how recently *the same tile*, rather than its pair, had been seen (**Figure 1**). We considered only match trials for this predictor (n-since-pair*match) because there was no successful retrieval of the tile's pair in mismatch trials.

Figure 5 shows an example electrode in the left middle temporal gyrus (arrow in **Figure 5E**). In contrast with the electrode in **Figure 4**, both the match predictor and the nsp predictor were significant in the GLM analysis (**Figure 5A**). The t-statistic for nsp was negative, indicating a *decrease* in gamma band power for matching pairs that were more distant in memory. Indeed, responses were strongest for those tiles whose pairs had been seen less than 2 clicks ago (**Figure 5B**, red) and weakest when matching pairs had been seen more than 10 clicks ago (**Figure 5B**, purple). There was a negative correlation between the area under the curve (AUC) of the gamma band power and nsp (**Figure 5C**, $p<0.001$, linear regression). This correlation disappeared when considering mismatch trials (**Figure 5D**, $p=0.66$, linear regression), suggesting that the relationship between the neural signals and memory strength was contingent on successful retrieval.

The nsp predictor was statistically significant ($p<0.01$, GLM) in 15 electrodes in the gray matter (2.2% of the total, **Table S6A**, **Figure 5E**) and 9 electrodes in the white matter (1.8% of the total, **Table S6B**, **Figure S10E**). For an example electrode located in the white matter, see **Figure S10**. Most of these electrodes showed a negative t-statistic, as in the example in **Figure 5**, and three electrodes (20%) showed the reverse effect (i.e., an increase in the neural signal for more

311 distant associative memories). For most of these electrodes (73.3%), *match* was also a significant
312 predictor, as illustrated by the example in **Figure 5A**, indicating that the neural signals encoded
313 *both* successful retrieval *and* memory strength.
314
315 **Neural signals reflect feedback after the second tile**
316
317 We have thus far focused on describing the responses elicited by the first tile in each trial.
318 Next, we evaluated the neural responses triggered by the click of the second tile. We first asked
319 whether novelty and familiarity were also encoded in the neural responses after the 2nd tile. We
320 built a separate GLM using the same 15 predictors except for n-since-pair*match (**Table 1**) to
321 describe the AUC of the gamma power during one second after clicking the 2nd tile. We excluded
322 n-since-pair*match here because it would always be 1 during match trials (by definition, the first
323 click was the pair of the second click). For the second tile, first-click was a significant predictor in
324 24 electrodes in the gray matter (3.6% of the total, **Table S7A**, **Figure S11E**) and 12 in the white
325 matter (2.4% of the total, **Table S7B**). Thus, less than half the number of electrodes reflected
326 novelty during the 2nd tile compared to the first tile (cf. **Table S7A** versus **Table S3A** and **Table**
327 **S7B** versus **Table S3B**). For the second tile, *n-since-last-click* was a significant predictor in 9
328 electrodes in the gray matter (1.3% of the total, **Table S8A**, **Figure S11D**) and 24 in the white
329 matter (4.9% of the total, **Table S8B**), again, less than half the number of electrodes reflecting
330 familiarity during the first tile (cf. **Table S8A** versus **Table S4A** and **Table S8B** versus **Table S4B**).
331 An example electrode in the LOF region whose responses correlated with familiarity after
332 the 2nd tile is shown in **Figure S11**. The LOF cortex contained significantly more electrodes than
333 expected by chance ($p<0.01$, **Methods**). Among all the 9 electrodes where n-since-last-click was
334 a significant predictor during the 2nd tile, 7 electrodes also had first-click as a significant predictor
335 (**Figure S11D-E**, red circles). In sum, novelty and familiarity of a tile were still encoded in the
336 neural responses to the second tile, but to a lesser degree than during the responses to the first
337 tile. This reduction may be due to the fact that two images were presented simultaneously, and
338 the neural signals might reflect a weighted combination of the responses to each[64]. Moreover,

339 for match trials, the information about the 2nd tile does not need to be encoded in memory
340 anymore to thrive in the task.

341 Among the 83 electrodes that had first-click as a significant predictor during the 1st tile
342 and the 36 electrodes during the 2nd tile (including both gray and white matter), 15 electrodes
343 (11 gray matter + 4 white matter) overlapped, i.e., first-click was a significant predictor during
344 both the 1st and the 2nd tiles. Among the 77 electrodes that had n-since-last-click as a significant
345 predictor during the 1st tile and the 33 electrodes during the 2nd tile (including both gray and
346 white matter), 20 electrodes (5 gray matter + 15 white matter) overlapped, i.e., nslc was a
347 significant predictor during both the 1st and the 2nd tiles. These electrodes may reflect general
348 rather than specific novelty or familiarity mechanisms, irrespective of tile order, image content,
349 or location.

350 Next, we asked whether the differences between match and mismatch trials were also
351 manifested *after* the 2nd tile was revealed, i.e., after the participant became explicitly aware of
352 whether the trial was a match or not. **Figure 6** shows an example electrode located in the left
353 insula (see arrow in **Figure 6E**) where match was a significant predictor for the neural responses
354 after the 2nd tile ($p<0.001$, GLM, **Figure 6A**). The neural signals during match trials were larger
355 than during mismatch trials (**Figure 6B**) and could be readily observed even in single trials (**Figure**
356 **6C** vs. **7D**).

357 After the 2nd tile, the match predictor was statistically significant ($p<0.01$, GLM) for 112
358 electrodes in the gray matter (16.6% of the total, **Table S9A**, **Figure 6E**) and 66 electrodes in the
359 white matter (13.4% of the total, **Table S9B**, **Figure S12E**). For an example electrode in the white
360 matter, see **Figure S12**. The locations of all these electrodes, shown in **Figure 6E** (gray matter)
361 and **Figure S12E** (white matter), reveal that the majority were circumscribed to the LOF and the
362 insula. The proportions of significant electrodes in both regions were higher than expected by
363 chance ($p<0.01$, **Methods**).

364 There were 17 electrodes in the gray matter and 15 in the white matter where the match
365 predictor was significant for both the 1st and the 2nd tiles. These electrodes represented 53.1%
366 (gray matter) and 50% (white matter) of the electrodes that were significant according to the 1st
367 tile, and 15.2% (gray matter) and 22.8% (white matter) of the electrodes that were significant

368 according to the 2nd tile. These electrodes were located in the lateral orbitofrontal cortex, the
369 medial temporal lobe, and the insula (**Figure 4E**, **S6E**, **7E**, and **S11E**, red circles). The electrode in
370 **Figure S12** exemplifies such responses (compare the difference between match and mismatch
371 before the onset of the 2nd tile in **Figure S12B** versus **Figure 6A**). The electrode in **Figure S9** reveals
372 a continuous enhancement for match trials after the 1st tile that was sustained and continued
373 after the onset of the 2nd tile.
374
375 **A machine learning classifier could predict matches in single trials**
376
377 We evaluated whether the neural responses within a brain region could predict if a trial
378 was a match or a mismatch (**Methods**). For this analysis, we considered only those brain regions
379 with more than 12 electrodes combining all participants (**Methods**). **Figure 7** shows the average
380 decoding performance of an SVM classifier after 200 iterations of 5-fold cross-validation. At each
381 iteration, the SVM consisted of a binary classifier (match versus mismatch). The predictors were
382 the PCA features extracted from the concatenated neural responses of electrodes within a
383 particular brain region. The superior parietal gyrus and insula exhibited decoding accuracy above
384 chance ($p<0.01$, **Methods**) during the 1st tile (**Figure 7A**). The lateral orbitofrontal and middle
385 temporal cortex also showed accuracy above chance (>60%, **Figure 7A**), albeit not statistically
386 significant. As expected based on the responses of individual electrodes, the decoding accuracy
387 was higher after the 2nd tile compared to the 1st tile. After the 2nd tile, multiple brain regions
388 showed accuracy above chance ($p<0.01$, **Figure 7B**). The lateral orbitofrontal cortex, insula,
389 middle temporal gyrus, and pars opercularis showed the highest accuracy (>75%). Similar results
390 were obtained when subsampling 12 electrodes during each iteration (**Figure S13**).
391
392 **A computational model provides a first-order approximation to the behavioral and neural**
393 **measurements**
394 To further understand the mechanisms at play during the task, we built a computational
395 model that focused on the storage and retrieval of information (**Figure 8**, **Methods**). The
396 computational model consists of a Hebbian attractor neural network with all-to-all connectivity.

397 The units are divided into position units (the number equaling the number of tiles on the board)
398 and label units (the number equaling the number of images on the board) (**Figure 8A**). The model
399 has two main modes of operation: learning (**Figure 8B**), and inference (**Figure 8C-D**). After the
400 first click, the model receives as input the label of the tile and its position. The activity of each
401 unit evolves over time based on the external input and the weighted input from other units
402 followed by a rectifying non-linearity and normalization (**Methods**, Equation 1). Concomitantly,
403 the weights are updated in a Hebbian manner (**Methods**, Equation 2). During inference, the
404 model selects the position unit with the maximum activation for the second click. The model
405 proceeds in this manner until all matches have been found.

406 We computed the same performance evaluators from **Figure 2A**,**B**,**D,F** for the model. We
407 did not compute the metrics for **Figure 2C,E** because the model chooses the first tile randomly
408 among the available tiles (**Methods**). We defined the reaction time as the number of steps
409 needed for the selected unit to reach 0.9 of its maximum value (**Methods**). The number of clicks
410 per tile increased with the board size, approximating the participants' behavior (compare **Figure**
411 **9A** versus **Figure 2A**). The reaction time for the model was longer for mismatch trials than for
412 match trials for all board sizes ($p<0.001$, compare **Figure 9B** versus **Figure 2B**). The nslc value
413 increased with board size and was much larger for mismatch trials compared to match trials,
414 consistent with the participants' behavior ($p<0.001$, compare **Figure 9C** versus **Figure 2D**).
415 Similarly, the nsp value increased with board size and was also significantly larger in mismatch
416 trials compared to match trials for all board sizes ($p<0.001$, compare **Figure 9D** versus **Figure 2F**).

417 To investigate the model's inner workings, we defined two metrics based on the unit
418 activations. First, to compare with the match related signals in **Figure 3**, we computed an overall
419 maximum energy (**Methods**, Equation 3). This maximum energy was smaller for trials with nslc=1
420 ($p<0.001$, **Figure 9E**), reflecting a strong correlate of memory for recently seen tiles (compare to
421 **Figure 3B** and especially **Figure 3F**). Second, we defined a confidence metric by assessing the
422 relative activation for the strongest unit with respect to the other units during the inference step
423 (**Methods**). The confidence metric was significantly larger for match trials compared to non-
424 match trials ($p<0.01$, **Figure 9F**), which was qualitatively similar to the neural responses described
425 in **Figure 5**.

426

427 **Discussion**

428

429 In this study, we investigated the dynamics of neural signals during a natural memory task
430 where participants engaged in a classical card-matching game. Participants performed the task
431 well, slightly worse than expected by a perfect memory model (**Figure 2A**), showing increased
432 reaction times during mismatch trials (**Figure 2B**) as well as decay of memory traces with time
433 since encoding (**Figure 2C-F**).

434 Many studies have focused on studying memory for a list of sequentially presented stimuli
435 [1,7,12,19,24,65,66] or examined memory in naturalistic or real-world scenarios at the behavioral level
436 [67-71]. The task introduced here strikes a balance between these two approaches, presenting a
437 more realistic and complex setting that involves associative and non-associative memories within
438 the same task and introducing task-dependent complexity compared to word lists. Yet, our task
439 allows for a high level of control over stimulus timing and experimental parameters that are
440 difficult to achieve when studying memory in real-world scenarios.

441 Complex and natural tasks necessarily depend on the interplay of multiple intercorrelated
442 variables. To tame the complexity of these different variables, we used generalized linear models
443 (GLMs) to quantitatively assess the influence of distinct predictors on the neural responses.
444 Through these GLM analyses, we could characterize neurophysiological responses that were
445 largely governed by individual predictors after accounting for the correlations among predictors
446 (**Figure S4**). While focusing on any one predictor, these results were corroborated by subsampling
447 the data to equalize other predictor variables that could potentially affect the neural responses.
448 The extensive sampling of brain regions, including neural activity from more than 1,000
449 electrodes across 20 participants (**Figure S2-S3**), allowed us to track neural responses during each
450 of the steps required in the task with broad brain coverage.

451 The first step to encode tile information is to correctly determine whether a tile is novel
452 or not. We refer to the ability to detect novelty and familiarity as non-associative recognition
453 memory[16,24]. Assessment of novelty and familiarity orchestrate strategies of encoding and
454 maintenance of information in memory[1,72]. We found strong neural responses that signal novelty

455 and familiarity (**Figure 3**, **Figure S5-6**, **S10-11**, **Table S3**, **S4**, **S7** and **S8**). Several electrodes
456 responded both to novelty and familiarity, showing similar responses to novel and highly
457 unfamiliar items (**Figure 3F-G** and **Figure S5B-C**). The lateral orbitofrontal cortex, the pars
458 opercularis, and the medial temporal lobe contained a preponderance of electrodes signaling
459 novelty and familiarity. These responses are reminiscent of novelty and familiarity signals that
460 have typically been described in tasks involving a sequence of images presented with occasional
461 repetitions[6,16,18,66] but are not restricted to the medial temporal lobe. While some electrodes may
462 also encode information about the image content (**Figure 3E**), most of the electrodes signaling
463 novelty and familiarity were not content-specific, consistent with the observation that neurons
464 involved in memory formation are rarely sharply tuned to particular sensory features[28].

465 After seeing the first tile in a trial, participants could estimate whether they remembered
466 the location of its pair and, thus, whether they would get a match or not. Participants link the
467 first tile with its pair to internally predict where to click next. Indeed, neural responses strongly
468 reflected not only these predictions (**Figure 4**, **Figures S7**-**9**) but also the internal estimate of the
469 memory strength or the confidence of these predictions (**Figure 5**). Even though participants
470 could not know for sure yet whether the trial would be a match or not, the neural signals
471 exhibited large differences between match and mismatch trials after the first tile and before the
472 revelation of the second tile. These differences were either transient (**Figure 4**) or sustained
473 (**Figure S9**). We speculate that transient increases in activity during match trials might signal the
474 sudden realization and high confidence about the trial outcome (match or mismatch). In contrast,
475 sustained responses may correspond to the active retrieval processes. It is possible that sustained
476 activity could arise due to averaging across temporally shifted transient activities from individual
477 neurons[73]; however, it has been reported that single neurons in the hippocampus can also show
478 sustained firing rate increase for successful associative retrieval[74]. Extensive work has
479 documented the importance of the hippocampus and surrounding structures in the MTL in
480 associative memory (e.g.,[16,26,74,75]). In addition to the MTL, the current results show that other
481 areas, such as the lateral orbitofrontal cortex, also play a critical role in associative recall.

482 Several studies have highlighted the potential for attractor-based models to characterize
483 working memory processes[47,49,76,77]. Here we show as a proof-of-principle that a simple

instantiation of an attractor-based neural network model can qualitatively capture the properties of human participants both at the behavioral level (**Figure 9A-D**) and also at the neural level (**Figure 9E-F**). This basic neural network architecture can be readily linked to a visual neural network backbone to further examine the underlying representation of visual signals in working memory. Additionally, the model could be extended to examine even more complex tasks that involve multiple-way associations and dynamic changes in the structure of the environment over time. The high temporal resolution, extensive spatial sampling, and computational models provide an opportunity to characterize the dynamics of complex naturalistic tasks. These observations provide initial steps to further our understanding of how different components of encoding and retrieval interact during the formation of natural memory events.

Methods

Task paradigm

Participants performed our implementation of the classical memory matching game (**Figure 1, Movie S1**). The game involves remembering the location and content of a set of tiles to find all the matching pairs. A square board containing $n \times n$ tiles was shown throughout each block. In the beginning, all tiles were shown in black. In each trial, participants chose one tile, and then a second tile, by clicking on them in a self-paced fashion. Upon clicking, the tile revealed a common object like a cat or an indoor scene like a kitchen. At the end of each trial, either the two tiles revealed the same content (match) or not (mismatch). If the tiles matched, then the two tiles turned green 1,000 ms after the second click, and the two tiles could not be clicked again for the remainder of the block. If the tiles did not match, they turned black 1,000 ms after the second click and could be clicked again in subsequent trials. When all tiles turned green, i.e., all matches were found, the block ended, and another block began. During each block, the map between positions and objects was fixed. The game always started with a block of size 3×3 and progressed to more difficult blocks (4×4, 5×5, 6×6, and finally 7×7). Blocks with an odd number of tiles (3×3, 5×5, and 7×7) contained one distractor object (a human face) with no corresponding pair. For each block except the 3×3 board, there was a limit for the total time elapsed (2 minutes for 4×4,

513 3.3 min for 5×5, 4.8 min for 6×6, and 8.2 min for 7x7). If a participant did not complete a block
514 within the time limit, the block ended, and a new, easier block started by reducing the board size
515 *n* by 1, except when *n*=7, where it was reduced by 2. Conversely, when participants successfully
516 completed a block with a board of size *n* within the allotted time limit, they moved on to a more
517 difficult block by increasing *n* by 1. When participants completed an *n*=7 block, they performed
518 further *n*=7 blocks. There was no image repetition across blocks.

519 All the images were from the Microsoft COCO 2017 validation dataset [78] and were
520 rendered in grayscale and square shape. We included a balanced number of pictures from 5
521 categories: person, animal, food, vehicle, and indoor scenes. All the images were rendered on a
522 13-inch Apple MacBook Pro laptop. The size of each tile was 0.75×0.75 inches (approximately 2x2
523 degrees of visual angle, dva) and the separation between two adjacent tiles was 0.125 inch (0.33
524 dva) for board size *n*=7 and 0.25 inch (0.67 dva) for the others. The game implementation was
525 written and presented using the Psychtoolbox extension [79,80] in Matlab_2016b (Mathworks,
526 Natick, MA).

527

528 **Epilepsy participants and recording procedures**

529 We recorded intracranial field potentials from 20 patients with pharmacologically
530 intractable epilepsy (12-52 years old, 9 female, **Table S1**) undergoing monitoring at Boston
531 Children's Hospital (Boston, US), Brigham and Women's Hospital (Boston, US), and Xuanwu
532 Hospital (Beijing, China). All recording sessions were seizure-free. All patients had normal or
533 corrected-to-normal vision. The study protocol was approved by each hospital's institutional
534 review board. Experiments were run under patients' or their legal guardians' informed consent.
535 One patient at Brigham and Women's Hospital (BWH) was implanted with both stereo
536 encephalography (sEEG) and electrocorticography (ECoG) electrodes, while all other patients had
537 only sEEG electrodes (Ad-tech, USA; ALCIS, France). Intracranial field potentials were recorded
538 with Natus (Pleasanton, CA) and Micromed (Italy). The sampling rate was 2048 Hz at Boston
539 Children's Hospital (BCH), 512 Hz or 1024 Hz at BWH, and 512 Hz at Xuanwu Hospital (XWH).
540 Electrode trajectories were determined based on clinical purposes for precisely localizing
541 suspected epileptogenic foci and surgically treating epilepsy[81].

542

543 **Eye tracking procedures**

544 Ten non-epilepsy healthy participants (23-35 years old, 9 female) performed the same
545 task while their eye movements were tracked with the EyeLink 1000 plus system (SR Research,
546 Canada) at a sampling rate of 500 Hz. The task paradigm was the same as the one for epilepsy
547 participants except that, before each block began, participants fixated on a center cross to ensure
548 that the EyeLink eye-tracking system was well-calibrated. Otherwise, a re-calibration session
549 ensued. The task was presented on a 19-inch CRT monitor (Sony Multiscan G520), and
550 participants sat about 21 inches away from the monitor screen. The tile size was 1x1 inches
551 (approximately 2.7x2.7 degrees of visual angle) as appeared on the screen. The study protocol
552 was approved by the institutional review board at Boston Children's Hospital, and each
553 participant completed the task with informed consent. All participants had normal or corrected-
554 to-normal vision. All participants completed 16 blocks.

555

556 **Behavioral analyses**

557 We created two computational models to simulate behavior assuming perfect memory
558 or no memory (chance performance, **Figure 2A**). The perfect memory model remembered all
559 revealed tiles without forgetting. The random model simulated random clicking. We calculated
560 the reaction time (RT, time between two clicks in a trial), n-since-pair (number of clicks since the
561 last time when a tile's matching pair was seen), n-since-last-click (the number of clicks since the
562 same tile was clicked), and n-times-seen (number of times the same image had been seen). For
563 n-since-pair and n-since-last-click, we excluded trials in which any tile was seen for the first time,
564 i.e., when a tile's matching pair had never been revealed, or there was no previous click. We
565 compared these variables for match and mismatch trials at each board size (**Figure 2**,
566 permutation test, 5,000 iterations, α=0.01). We defined random matches as a match trial where
567 the second tile had never been seen before; such trials were excluded from both the behavioral
568 and neurophysiological analyses. We used the F-test for linear regression models to assess
569 whether RT, n-since-pair, n-since-last-click, and n-times-seen significantly covary with board size.
570 The linear regression models' predictors were these four behavioral parameters and the

571 dependent variable the board size. We created separate models for match and mismatch trials
572 and 1st and 2nd tiles.
573
574 **Electrode localization**
575 Electrodes were localized using the iELVis[82] toolbox. We used Freesurfer[83] to segment the
576 preimplant magnetic resonance (MR) images, upon which post-implant CT was rigidly registered.
577 Electrodes were marked in the CT aligned to preimplant MRI using Bioimage Suite[84]. Each
578 electrode was assigned to an anatomical location using the Desikan-Killiany[85] atlas for subdural
579 grids or strips or FreeSurfer's volumetric brain segmentation for depth electrodes. For white
580 matter electrodes, we also reported their closest gray matter locations. Out of 1,750 electrodes
581 in total, we included 676 bipolarly referenced electrodes in the gray matter (**Figure S2, Table S2**)
582 and 492 bipolarly referenced electrodes in the white matter (**Figure S3, Table S2**). Five hundred
583 and eighty-two electrodes were not considered for analyses due to bipolar referencing, locations
584 in pathological sites, or electrodes containing large artifacts. Electrode locations were mapped
585 onto the MNI305 average brain via affine transformation[86] for display purposes (e.g., **Figure S2-**
586 **S3**).
587
588 **Preprocessing of intracranial field potential data**
589 Bipolar subtraction was applied to each pair of neighboring electrodes on each shank of
590 depth electrodes or subdural grids/strips[87]. A zero-phase digital notch filter (Matlab function
591 "filtfilt") was applied to the bipolarly subtracted broadband signals to remove the line frequency
592 at 60 Hz (BCH, BWH) or 50 Hz (Xuanwu) and their harmonics. For each electrode, trials whose
593 amplitudes (Voltage_{max}-Voltage_{min}) were larger than 5 standard deviations from the mean
594 amplitude across all trials were considered potential artifacts and discarded from further
595 analyses [88]. For the first tile, the time window for artifact rejection was from 400 ms before the
596 click until 1 second after the average RT. For the second tile, the time window was [400 ms +
597 average RT] before the second click until 1 second after the second click. Across all electrodes,
598 we rejected 1.75% of all trials for the 1st tile and 1.73% for the second tile.
599

600 **Time-frequency decomposition**

601 The gamma band (30-150 Hz) power was computed using the Chronux toolbox[89]. We used
602 a time-bandwidth product of 5 and 7 leading tapers, a moving window size of 200 ms, and a step
603 size of 10 ms[90]. For each trial, the power was normalized by subtracting the mean gamma band
604 power during the baseline (400 ms before 1st tile) and dividing by the standard deviation of the
605 gamma power during the baseline. For all the participants, there were more mismatch than
606 match trials. In the raster plots, we subsampled the mismatch trials, keeping those trials whose
607 reaction times were closest to the mean reaction time of match trials. All random matches were
608 excluded from analyses.

609

610 **Generalized linear model**

611 We used generalized linear models (GLM)[91,92] to analyze the relationship between the
612 gamma band power and behavioral parameters. We used two different GLMs, one using neural
613 responses between the 1st and the 2nd tiles and the other using neural responses after the 2nd tile.
614 For the first GLM, the time window started when the 1st tile was clicked and ended at a time
615 corresponding to the 90th percentile of the distribution of reaction times (time difference
616 between the 1st and the 2nd click, **Figure 1A**) for each participant. This criterion was a reasonable
617 tradeoff between minimum overlap with responses after the 2nd tile and the maximum amount
618 of information captured. For the second GLM, we used 1 second after the 2nd tile click as the
619 analysis window. The response variable to be fit by the GLM analyses was defined as the area
620 under the curve (AUC) of the gamma band power over the specified time windows. **Table 1**
621 describes the behavioral parameters that were considered as predictors in the models.

622 We performed a multicollinearity analysis to assess the presence of highly correlated
623 predictors that could impair the model's performance[93,94]. We calculated the variance inflation
624 factor (VIF) for each predictor to detect the presence of multicollinearities. A VIF of 1 indicates
625 that there is no correlation with other predictors. The larger the VIF, the higher the correlation.
626 A VIF greater than 5 indicates a very high correlation that could significantly harm the model's
627 performance. For all participants in our analysis, the VIFs of all predictors were smaller than 3
628 (**Figure S4C-D**).

629 For n-since-pair, we included the interaction term between this predictor and match (n-
630 since-pair*match) to test the hypothesis that when a trial was a match, the strength of the neural
631 response after the first tile was modulated by how recently the tile's matching pair was seen for
632 the last time. The neurophysiological responses confirmed that this is a reasonable way to model
633 the data (**Figure 5B**). We represented image categories as predictor variables in the GLM by
634 including four out of the five categories (animal, food, vehicle, and person). We dropped the
635 "indoor" category to avoid falling into the "dummy variable trap"[95]. For each predictor, we
636 calculated the parameter estimate (beta coefficient) from the least mean squares fit of the model
637 to the data, the t-statistic (beta divided by its standard error), and the p-value to test the effect
638 of each predictor on the neural responses. A beta coefficient or t-statistic of zero indicated that
639 the predictor did not affect the neural responses. A predictor was considered statistically
640 significant if the GLM model differed from a constant model ($p<0.01$) and the p-value for that
641 predictor was smaller than 0.01.
642 To determine if any brain region contained significantly more electrodes than expected
643 by chance considering any GLM predictor, we randomly sampled the same number (n) of
644 electrodes as those where that predictor was significant, from the total electrode population
645 (separately for gray and white matter electrodes) for 5,000 iterations. Taking the *match* predictor
646 for gray matter electrodes as an example, from the total of 676 gray matter electrode locations,
647 we randomly sampled 32 electrodes (the number of match-significant gray matter electrodes)
648 5,000 times, and calculated the p-value of any location, say insula, as the number of times when
649 n for insula and match-significant was less than n for insula sampled. If $p<0.01$, that brain region
650 was considered to have significantly more electrodes than expected by chance.
651
652 **Decoding of match**
653 We used a machine learning decoding approach to evaluate whether the neural
654 responses from a given brain region could predict whether the trial was a match or a mismatch.
655 For this analysis, we selected only those brain regions in which we had at least 12 electrodes. We
656 used two different decoders for each brain region, one using neural responses between the 1st
657 tile and 800 ms after the 1st tile click, and the other using the neural responses between the 2nd

658 tile and 800 ms after the 2nd tile click. We performed 200 iterations of 5-fold cross-validation for
659 each brain region and tile to split the trials into independent train and test sets (1,000 splits in
660 total). We concatenated the neural responses of electrodes within the same brain region, using
661 two different approaches: (i) taking all electrodes in each brain region, and (ii) randomly
662 subsampling 12 electrodes at each iteration. The number of match and mismatch trials was
663 normalized by random subsampling. To reduce the dimensionality of the neural responses, we
664 used principal component analysis (PCA). The PCA parameters were computed using only the
665 training data, and we selected the number of components that could explain 70% of the training
666 neural responses variance. We used support vector machines (SVM) with a linear kernel for the
667 binary classification (match or mismatch), using as the model inputs the PCA features computed
668 from the neural responses. We followed the same procedure to test whether the classification
669 performance was above chance, but we randomized the response variable (match or mismatch)
670 at every iteration. We calculated the p-value as the number of times when the accuracy using
671 random labels was above the average accuracy using the actual labels. If $p<0.01$, neural
672 responses of that brain region could predict match and mismatch above chance.
673
674 **Computational model**
675 We developed an attractor network model consisting of a fully connected recurrent
676 network with the number of units n equal to the number of tiles in the grid plus the number of
677 different images. For example, the model for the 3x3 board shown in **Fig 1A** was an attractor
678 network with n=3x3+5=14 units (**Figure 8**).
679 The units in the network were designed to model "where" and "what", i.e., position and
680 image labels. Let $\boldsymbol{x}_p$ be a vector of length equal to the number of tiles in the grid, $\boldsymbol{x}_l$ be a vector
681 of length equal to the number of different images in the grid, and $\boldsymbol{x}$ denote the concatenation
682 $[\boldsymbol{x}_p, \boldsymbol{x}_l]$ (**Figure 8A**). The input to the network is $\boldsymbol{x}$. Each entry in $\boldsymbol{x}_p$ and $\boldsymbol{x}_l$ can take the values -
683 1, 0, or 1. The state of the network at time t is denoted by the vector $\boldsymbol{h}_t = [\boldsymbol{p}_t, \boldsymbol{l}_t]$ of size n, where
684 $\boldsymbol{p}_t$ and $\boldsymbol{l}_t$ are the vectors of activations of the position and label units, respectively. Each entry
685 in $\boldsymbol{h}_t$ is a scalar value. The units in the network are connected in an all-to-all fashion and the
686 matrix $\boldsymbol{M}_t$ indicates the weights at time t ($\boldsymbol{M}_t \in \mathbb{R}^{n \times n}$).

The network stores memories in both persistent activities (active representations) and weights (silent representations)[49]. In contrast to the approach in ref.[49], which incorporates a bottleneck in the model to restrict its capacity, our model is devoid of any such bottleneck. Given an input $\boldsymbol{x}$ at time t, the network state and weights were updated similarly to ref.[96], according to:

$$\boldsymbol{h_t} = f\big(\mathcal{N}(\boldsymbol{x} + \boldsymbol{M}_{t-1}\boldsymbol{h}_t)\big) \qquad \text{Equation 1}$$

$$\boldsymbol{M}_t = \lambda \boldsymbol{M}_{t-1} + \eta \boldsymbol{h}_t \boldsymbol{h}_t^T \qquad \text{Equation 2}$$

Here $f(\cdot)$ is the LeakyReLU activation function and $\mathcal{N}(\cdot)$ is activation normalization. λ and η represent a decay rate for the previously stored memories and the learning rate for new memories, respectively. In line with ref.[96], activation normalization is expected to make the network more robust to the choice of the decay and learning rates. We note that the Hebbian learning is computed on the state of the network $\boldsymbol{h}_t$ rather than on the input $\boldsymbol{x}$. This means that the update of the memory matrix $\boldsymbol{M}_t$ is influenced by the interference between active and silent representations, thus limiting the network capacity. The hyperparameters were chosen by fitting the number of clicks per tile of the model to the participants' number of clicks per tile (**Figure 2A**). The results presented in this paper were obtained with $\lambda = 0.6$ and $\eta = 0.9$. Before the start of each board, the network weights were initialized uniformly at random in $[0,1]$, while the state of the network was initialized to 0. Changes in weights in neural networks are often interpreted as structural modifications to synaptic strengths. However, given the time scales involved in working memory tasks such as the one studied here, changes in $\boldsymbol{M}_t$ are more likely to reflect transient biophysical mechanisms such as synaptic facilitation rather than permanent structural synaptic modifications.

The model operates in two distinct regimes, which we refer to as *learning* (**Figure 8B**) and *inference* (**Figure 8C-D**). For each trial, the 1st tile was chosen at random among the available tiles. To simulate the task, for each trial the model performs learning→inference→learning. First, the model represents the position and label of the 1st tile. Second, the model performs inference on the label of the 1st tile. At the end of the inference regime, the most active neuron in $\boldsymbol{p}_t$ determines which tile to click (**Figure 8D**). Last, the model learns the position and label of the 2nd tile.

During learning (**Figure 8B**), the corresponding position entry of $\boldsymbol{x}_p$ is set to 1 and all other units are set to -1. Similarly, the corresponding label entry of $\boldsymbol{x}_l$ is set to 1 and all other units are set to -1. The network dynamics goes through 10 steps according to the two equations above. During inference (**Figure 8C-D**), the corresponding label of $\boldsymbol{x}_l$ is set to 1 and all the other units are set to 0. All the units of $\boldsymbol{x}_p$ corresponding to the available tiles are set to 0, while the ones corresponding to the unavailable tiles (those that have already been matched or already clicked in that trial) are set to -1. The network dynamics goes through 10 steps according to Equations 1-2. After these 10 steps, we select the unit with the maximum activation within the units of $\boldsymbol{x}_p$ corresponding to available tiles. If the second tile is a match, then those two tiles become unavailable in the next trials. The weight matrix $\boldsymbol{M_t}$, however, continues to include all the connections among all the units. The model proceeds until all tiles have been matched.

The number of clicks per tile, n-since-last-click and n-since-pair click for the 2nd tile were calculated for the model and compared to the participants' behavior (**Figure 9A-D**). To compute a proxy for the reaction time in the model, we used the same approach as in ref.[49], whereby the unit in $\boldsymbol{x}_p$ with the strongest activation during the inference time was selected and the reaction time was computed as the number of steps the unit takes to reach 0.9 of its maximum value.

To compare the inner workings of the model with the neural data, we defined two new metrics based on the unit activations. First, we defined the *max-energy* metric computed during the 1st learning phase of each trial, in analogy to the memory signals in **Figure 3**. The energy of the network was computed as:

$$E_t = -\boldsymbol{h}_t \boldsymbol{M}_t \boldsymbol{h}_t^T \qquad \text{Equation 3}$$

Min-max normalization was applied to the energy in each trial, and the maximum value in each trial was reported. The max-energy metric is shown in **Figure 9E**. Second, we defined a *confidence* metric that reflected the evidence for a match in a given trial, in analogy with the predictive signals shown in **Figure 5**. The confidence metric was defined by selecting the strongest activation in $\boldsymbol{p}_t$ during inference, subtracting the mean value of $\boldsymbol{p}_t$, applying min-max normalization to the difference, and then taking the maximum over time t in each trial. The confidence metric is shown in **Figure 9F**.

Data availability

We share all the deidentified psychophysics data, electrode location information, and neural data, together with all the code generated to model and analyze the data through the following public site: https://klab.tch.harvard.edu/resources/HowToGetAMatch.html

Author contributions: The task was designed by YX and GK. All the data were collected by RJW (XWH) and YX (BWH and BCH) with the help of PHW (XWH) and DW (BWH). GGZ (XWH), YZS (XWH), CRG (BWH), JRM (BCH), and SS (BCH) performed the surgeries on the patients. All the data were curated by YX and analyzed by YX and PSL, with frequent discussions with GK. The computational model was developed by RS, with frequent discussions with GK. The manuscript was written by YX, PSL, RS, and GK and approved by all authors.

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Figures and Tables

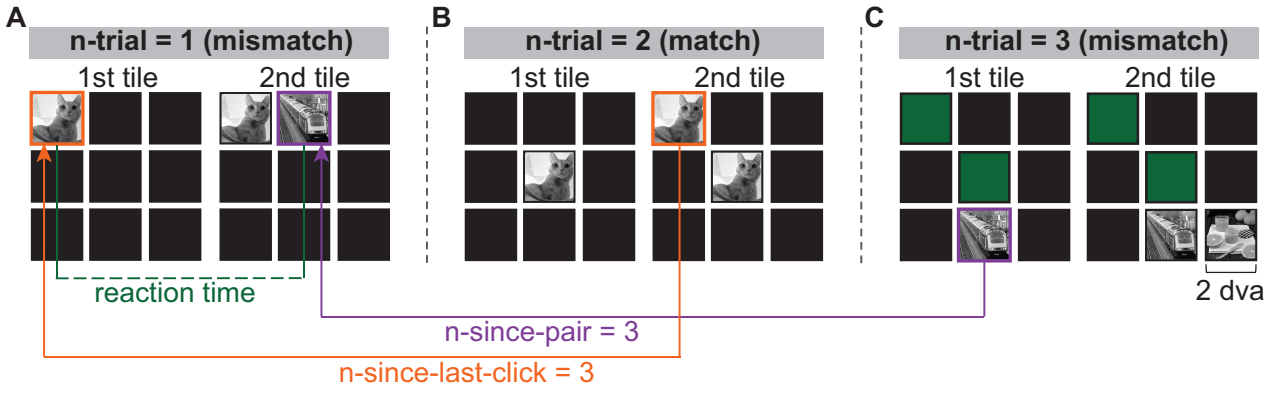

Figure 1. Experimental paradigm

A-**C.** Three consecutive trials in a 3×3 board. In each trial, two tiles were flipped sequentially in a self-paced manner (1st tile, then 2nd tile). If the two tiles contained different images (**A**, **C**, **mismatch**), both tiles reset to their original active (black) state after 1 second. If both tiles contained the same image (**B**, **match**), they turned green after 1 second and stayed green for the remainder of the block. Three behavioral predictors used in the generalized linear models (GLM) are defined here: reaction time (the time between the 1st and 2nd tile within a trial), n-since-last-click (the number of clicks elapsed since the same tile was clicked last), and n-since-pair (the number of clicks elapsed since the last time a given tile's matching pair was clicked). Each tile spanned approximately 2 degrees of visual angle (dva) in size. See also **Movie S1**.

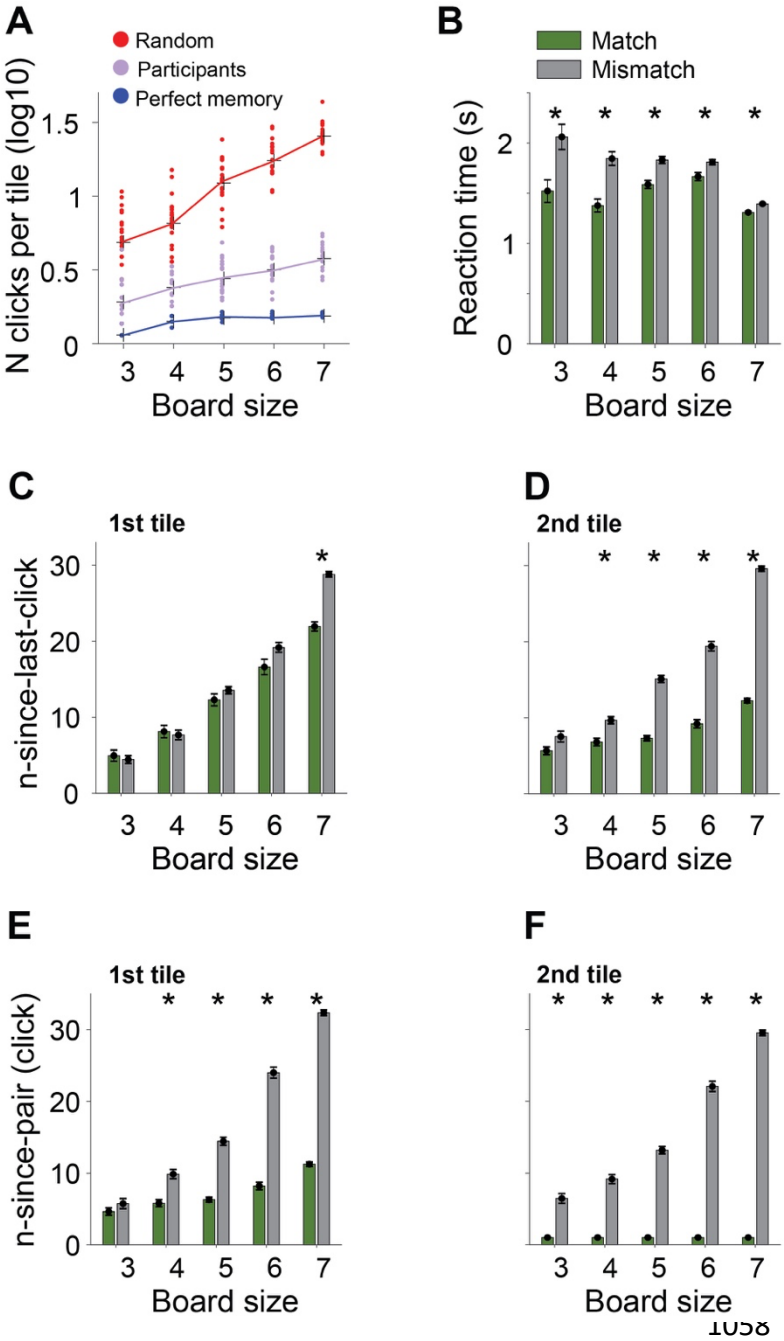

Figure 2. Behavioral measures show that participants thrived in the task and that finding matching pairs displayed classical memory effects

A. Number of clicks per tile (log scale) as a function of board size for random simulation model (red, n=20), perfect memory simulation model (blue, n=20), and epilepsy patient participants (purple, n=20) (**Methods**). Perfect memory simulation models may generate different number of clicks per tile because the click location for new tiles was randomized. The performance of epilepsy patients was better than the random model and worse than the perfect model. The number of clicks per tile increased as board size incremented. **B.** Reaction times for match (green) and mismatch (gray) trials for different board sizes. Asterisks denote significant difference between match and mismatch trials (permutation test, 5,000 iterations, α=0.01). Reaction time of mismatch trials was longer than match trials. **C-F.** Average n-since-last-click (**C**, **D**) and n-since-pair (**E**, **F**) for the 1st tile (**C**, **E**) and the 2nd tile (**D**, **F**) for each board size. Asterisks denote significant difference between match and mismatch trials (permutation test, 5,000 iterations, α=0.01). For n-since-last-click, trials in which a tile was clicked for the 1st time were excluded in this figure. For n-since-pair, trials in which any tile's matching pair had not been seen before were excluded in this figure. All error bars indicate s.e.m. (n=20 participants).

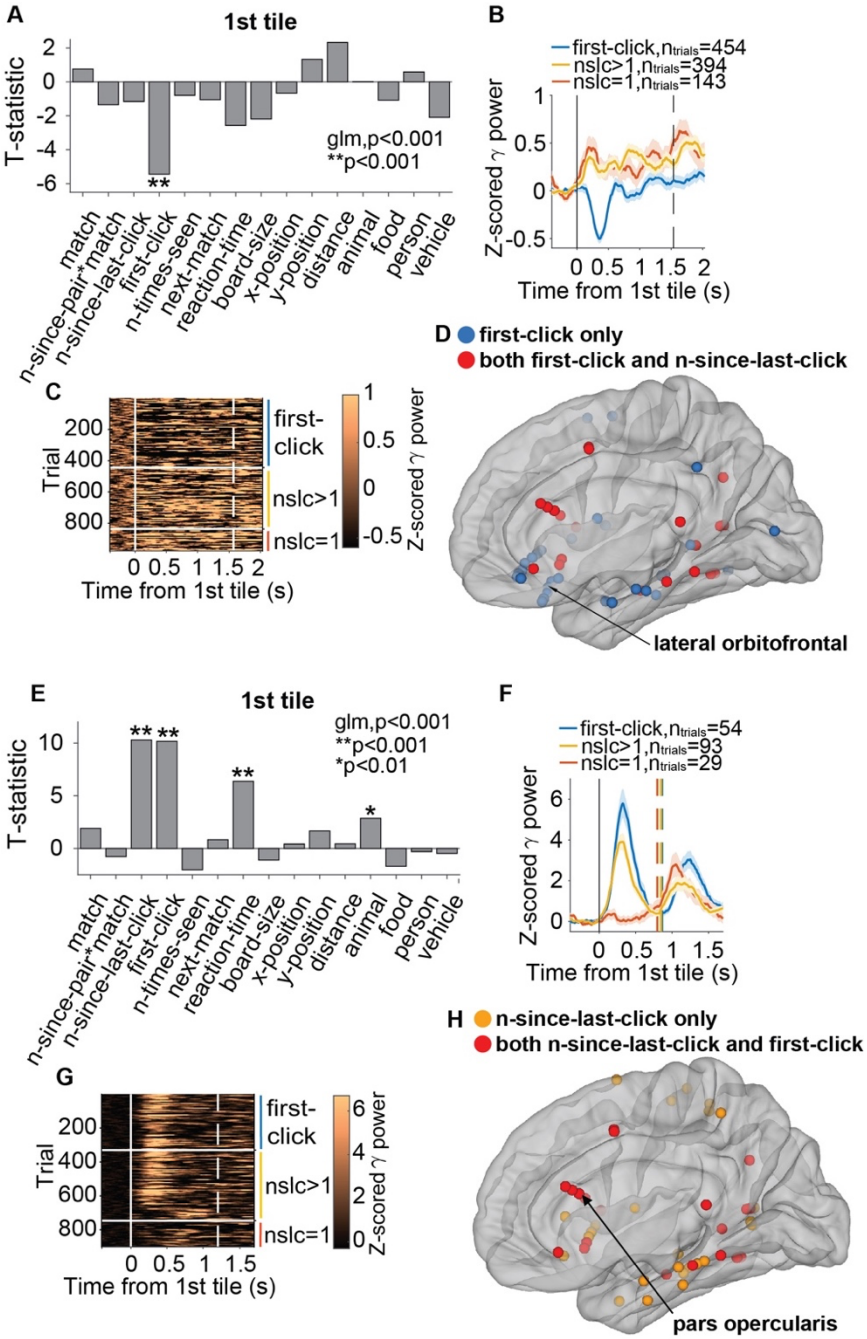

Figure 3. Neural signals reflect novelty and familiarity

Panels show two example electrodes, one in the right lateral orbitofrontal cortex (**A**-**D**), one in the left pars opercularis (**D**-**H**), and population locations in **D**, **H**.

A, **E**. T-statistic of each predictor in the GLM analyses (**Methods**). Asterisks indicate statistically significant predictors for the neural signals.

B, **F**. Z-scored gamma band power aligned to the 1st tile onset (solid vertical line) for novel tiles (blue), unfamiliar tiles (n-since-last-click>1, yellow), and familiar tiles (n-since-last-click=1, red). The vertical dashed line indicates the mean reaction time. Multiple dashed lines in **F** indicate reaction time equalization (**Methods**). The time axis extends from 400 ms before the click to 500 ms after the average reaction time. **F** displays only trials after RT equalization (**Methods**). Shaded error bars indicate s.e.m.

C, G. Raster plots showing the z-scored gamma power in individual trials ordered by first-click and then larger to smaller n-since-last-click; division indicated by white horizontal lines/spaces and colored vertical bars.

D. Locations of all electrodes where first-click was a significant predictor during the 1st tile. Blue: first-click only; red: both first-click and n-since-last-click were significant predictors.

H. Locations of all electrodes where n-since-last-click was a significant predictor during the 1st tile. Orange: n-since-last-click only; red: both n-since-last-click and first-click were significant predictors. All electrodes were reflected on one hemisphere for display purposes.

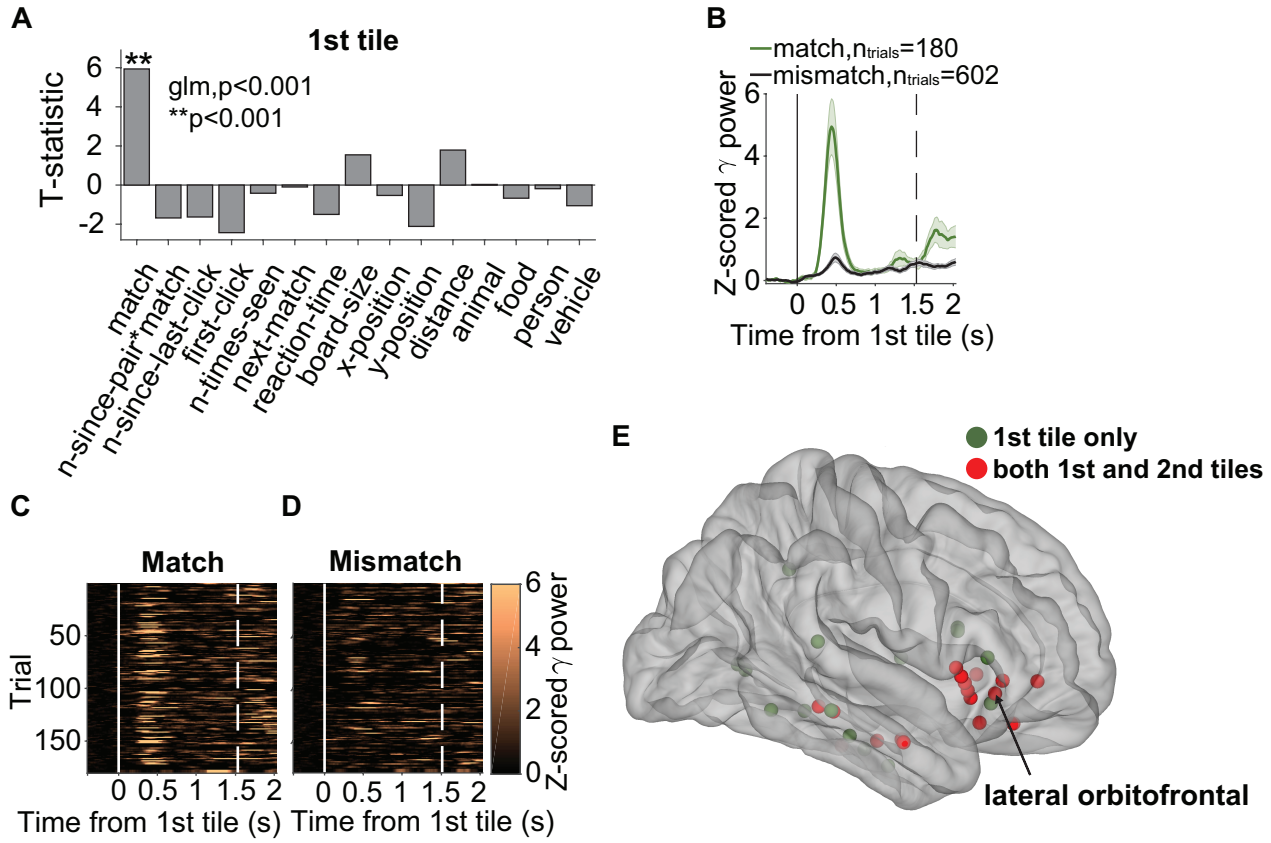

Figure 4. Neural signals predict correct retrieval

Panels show an example electrode in the right lateral orbitofrontal cortex (see arrow in part **E**) and population locations in **E**. The format follows **Figure 3**. **A.** T-statistic of each predictor in the GLM analysis. Asterisks indicate statistically significant predictors for the neural signals. **B**. Z-scored gamma band power aligned to the 1st tile onset (solid vertical line) for match trials (green) and mismatch trials (black). The vertical dashed line indicates the mean reaction time. Shaded error bars indicate s.e.m. **C**-**D**. Raster plots showing the gamma power in individual trials for match (left) and mismatch (right) trials. **E**. Locations of all electrodes where match was a significant predictor during the 1st tile only (green) and during both tiles (red). All electrodes were reflected on one hemisphere for display purposes.

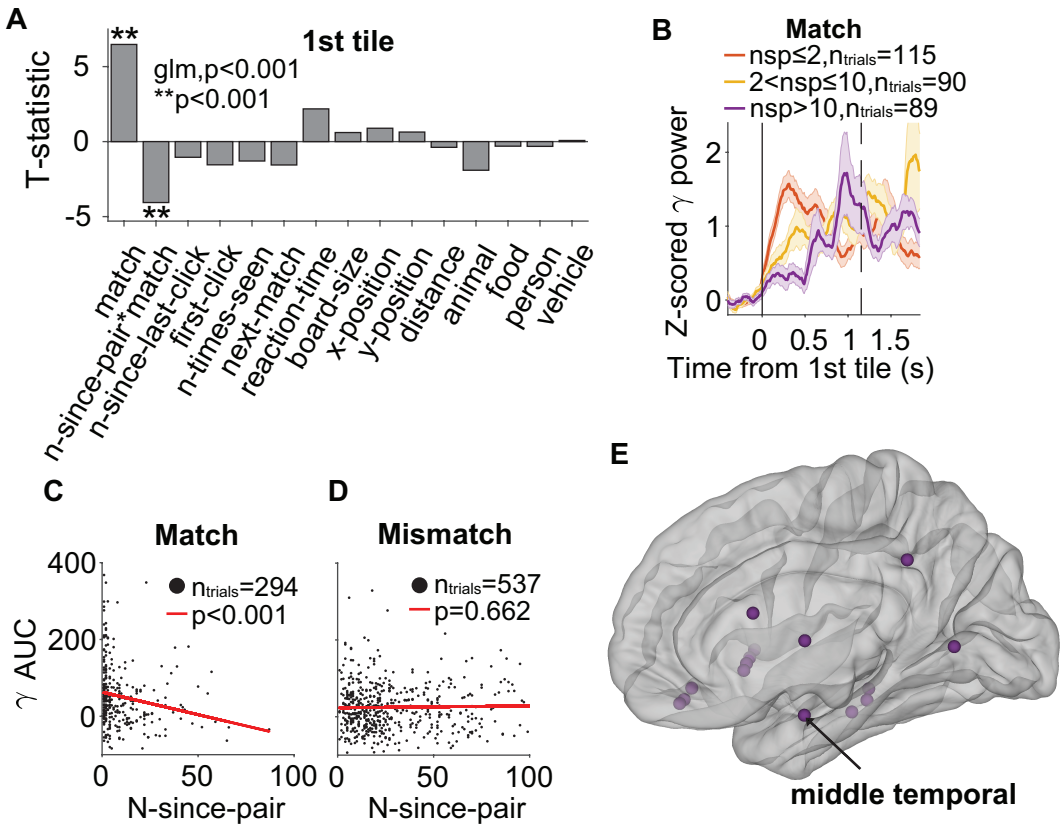

Figure 5. Neural signals reflect the strength of memory retrieval

Panels show an example electrode in the left middle temporal gyrus (see arrow in part **E**) and population locations in **E**. **A**. T-statistic of each predictor in the GLM analyses. Asterisks indicate significant predictors for the neural signals. **B**. Z-scored gamma band power aligned to the 1st file onset (solid vertical line) for match trials with small n-since-pair (nsp) (red, stronger memories), intermediate nsp (yellow), and large nsp (purple, weaker memories). The vertical dashed line indicates the mean reaction time. Shaded error bars indicate s.e.m. **C-D**. Scatter plots of the area under the curve (AUC) of the gamma band power as a function of nsp for match trials (**C**) and mismatch trials (**D**). Each dot represents one trial. Red lines show linear fits to the data. **E**. Locations of all electrodes where nsp was a significant predictor. All electrodes were reflected on one hemisphere for display purpose.

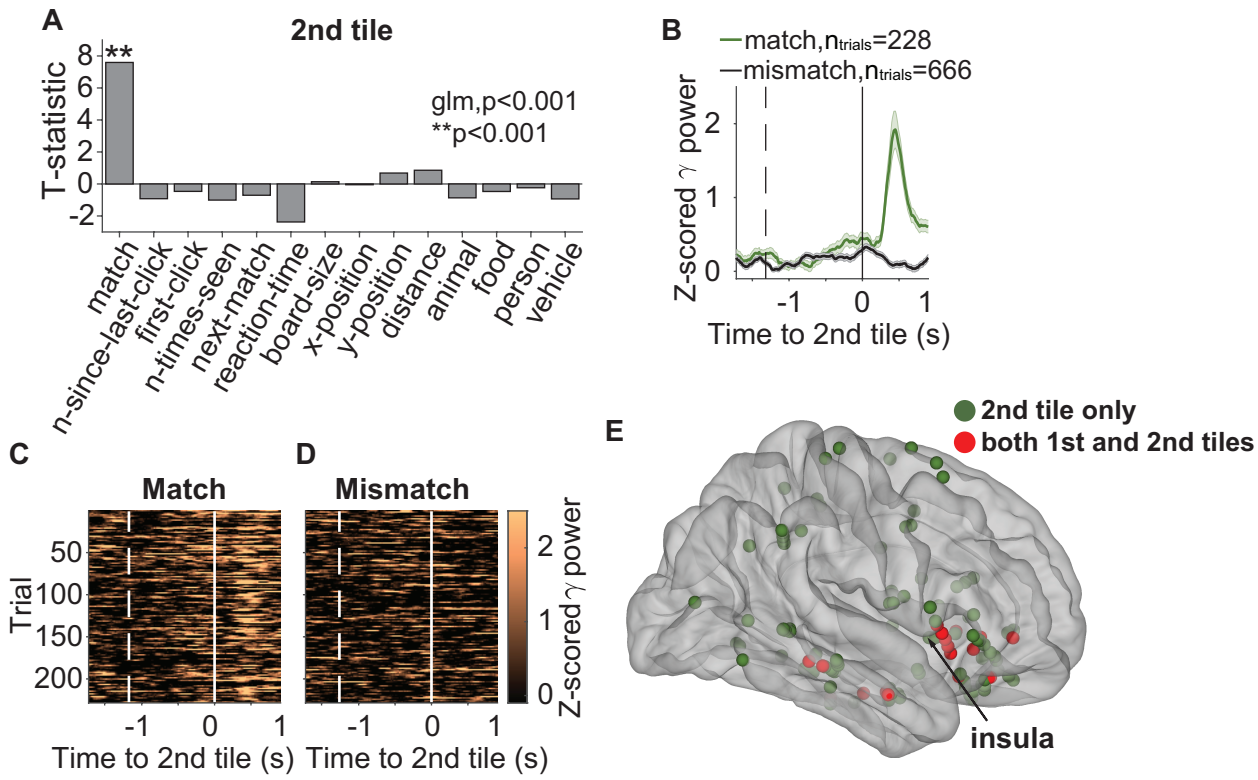

Figure 6. Neural signals after the second tile reflect correct retrieval

Panels show an example electrode located in the insula (see arrow in part **E**) and population locations. **A**. T-statistic of each predictor in the GLM analyses for the responses after the 2nd tile. Asterisks indicate significant predictors of neural signals. **B**. Z-scored gamma band power aligned to the onset of the 2nd tile (solid vertical line) for match (green) and mismatch (black) trials. The dashed line indicates the mean onset of the 1st tile. **C**-**D**. Raster plots showing the gamma band power in individual trials for match (left) and mismatch (right) trials. **E**. Locations of all electrodes where match was a significant predictor of neural responses after the 2nd tile only (green) or during both tiles (red). All electrodes were reflected on one hemisphere for display purpose.

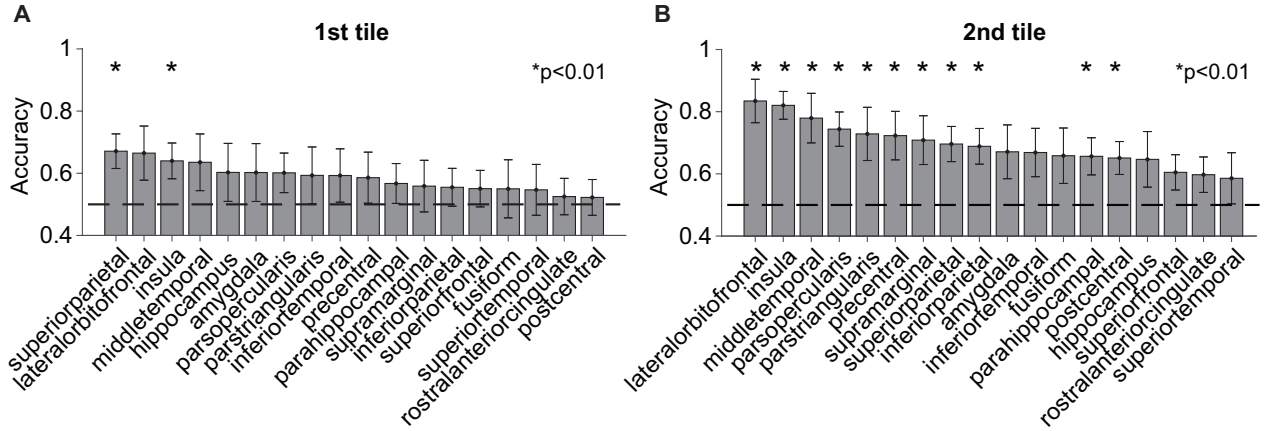

Figure 7. Machine learning decoding of match versus mismatch for all channels within each brain region

Average decoding accuracy for each brain region (**Methods**) using neural responses after the 1st tile (**A**) or after the 2nd tile (**B**). Brain regions are ordered from higher to lower average decoding accuracy. The dashed horizontal line indicates chance accuracy. Asterisks denote significant decoding accuracy above chance (α=0.01). All error bars indicate SD (n=1,000 iterations).

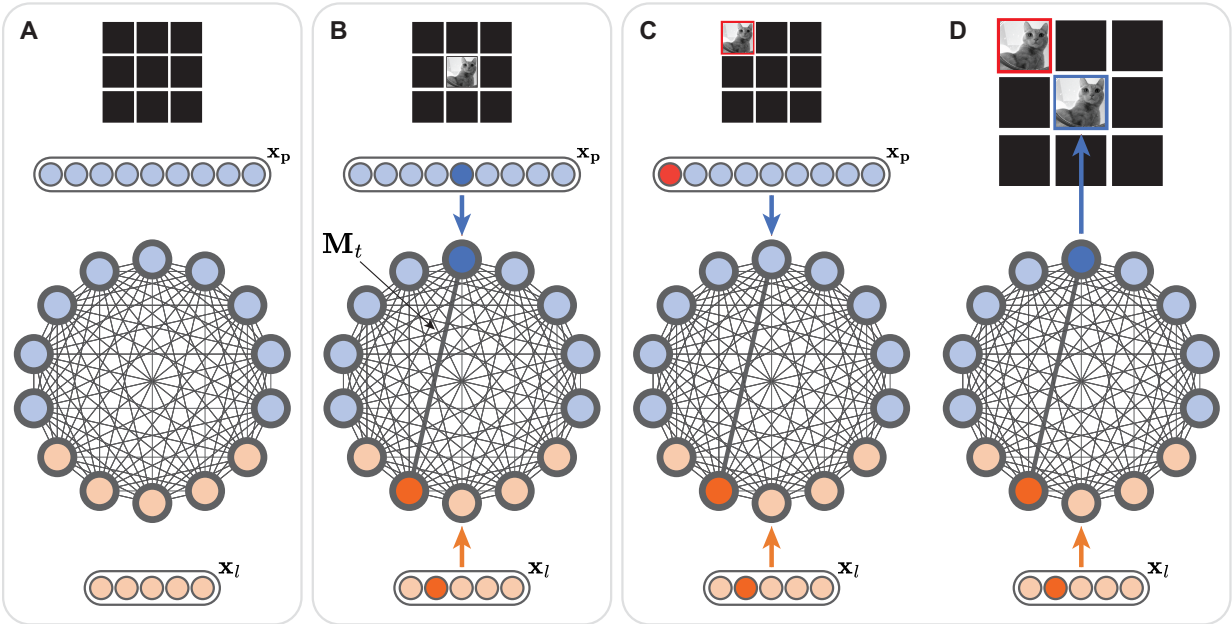

Figure 8: Hebbian attractor model architecture and operating regimes

A. Schematic representation of the model architecture used for the 3x3 grid. The 9 blue units encode position ($\boldsymbol{x}_p$), while the 5 orange units represent the image label ($\boldsymbol{x}_l$). The black lines between units illustrate the Hebbian weights $\boldsymbol{M}_t$ in the attractor network. **B.** Learning regime. In this example, the model represents a cat (label=2) at position=5. **C, D.** Inference regime. In this example, the model is tasked with matching the cat (label=2) observed at position=1. Only the label information is provided to the model in the inference regime. The model's updates (**Methods**) lead to the unit representing position=5 to exhibit the highest activity (**D**), thereby determining the corresponding tile to be clicked. The darker color indicates stronger activation of the corresponding units. The red color indicates the tile to match (which is unavailable for clicking, **Methods**) and its corresponding positional unit.

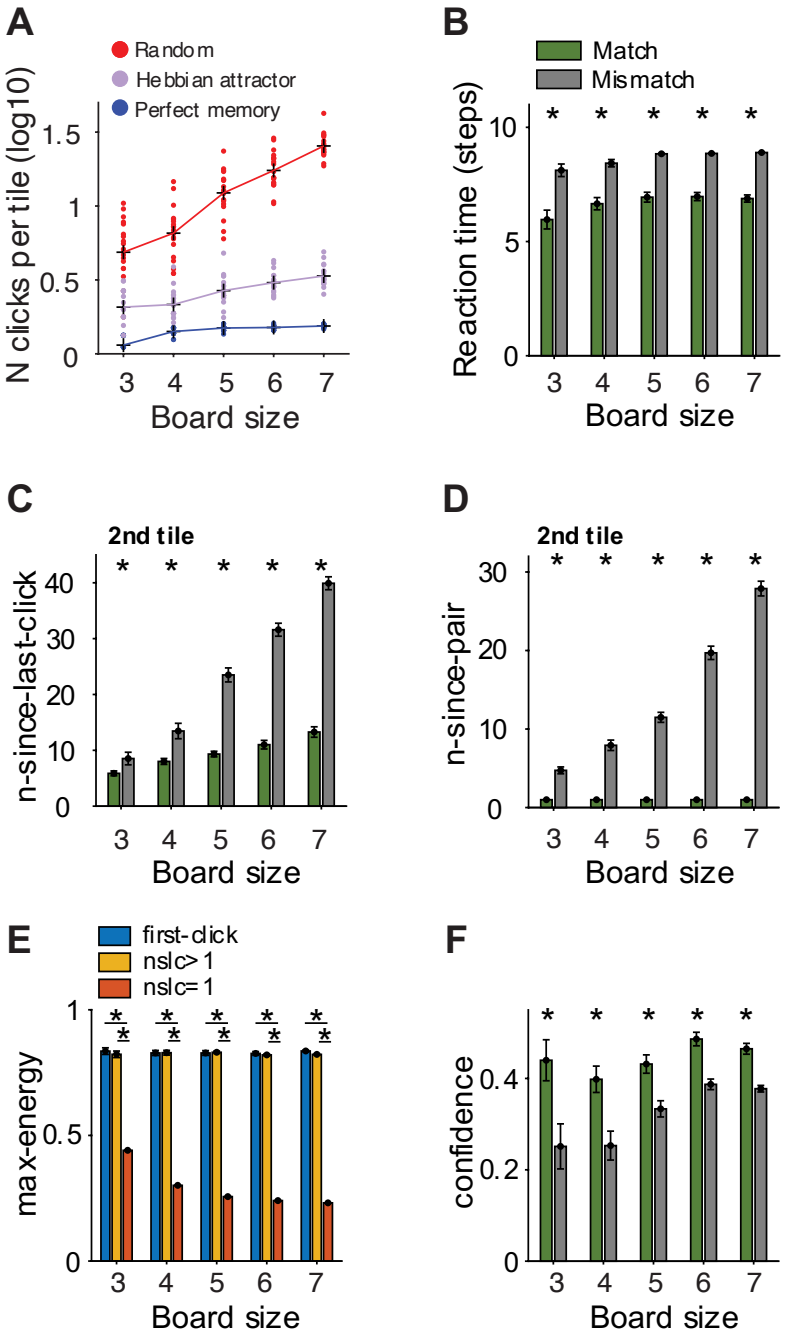

Figure 9: Hebbian attractor model captures behavior and neural measures

A. Number of clicks per tile (log scale) as a function of board size for random simulation model (red, n=20), perfect memory simulation model (blue, n=20), and Hebbian attractor (purple, n=20) (**Methods,** compare to **Figure 2A**). **B**. Reaction times of the model (Methods) for match (green) and mismatch (gray) trials for different board sizes (compare to **Figure 2B**). **C**, **D**. Average n-since-last-click (**C**) and n-since-pair (**D**) for the 2nd click for each board size (compare to **Figure 2D**, **F**. **E**). Max-energy for novel tiles (blue), unfamiliar tiles (n-since-last-click>1, yellow) and familiar tiles (n-since-last-click=1, red, compare to **Figure 3**). **F**. Model confidence for match (green) and mismatch (gray) trials for different board sizes (**Methods**). The model confidence in match trials was larger than in mismatch trials (compare to **Figure 5**). All asterisks denote significant

difference between match and mismatch trials (permutation test, 5,000 iterations, α=0.01). All error bars indicate s.e.m. (n=20).

Tables

Predictor	Description	Which tile
match	Whether the trial was a match or mismatch	both
n-since-pair*match	how many clicks ago the tile's pair was clicked (matched trials only)	1st
n-since-last-click	how many clicks ago the same tile was clicked	both
first-click	Whether a tile was clicked the very first time	both
n-times-seen	number of times the same image had been previously clicked	both
next-match	whether the next trial was a match or mismatch	both
reaction-time	time between the 1st and 2nd tile	both
board-size	Total number of tiles in the current block	both
x-position	x position in pixel	both
y-position	y position in pixel	both
distance	distance between the 2nd tile of the current trial and the 1st tile of the next trial in pixel	both
animal	image belonged to animal category	both
food	image belonged to food category	both
person	image belonged to person category	both
vehicle	image belonged to vehicle category	both

Table 1. Predictors in the generalized linear models, their definitions, and applicable tiles.

Supplementary Materials

The Supplementary Material (separate file) includes:

1 supplementary movie

9 supplementary tables

13 supplementary figures

Figure S1

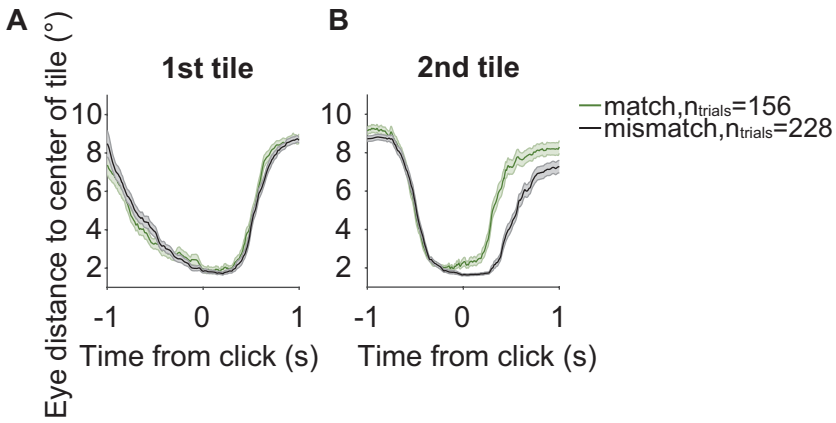

Figure S1. Participants' eye movements tracked the clicked locations.
Eye movements were similar during match and mismatch trials for the 1st tile, and for the 2nd tile before click time, but not for the 2nd tile after click time, when equalizing the reaction time and distances between the 1st and 2nd tiles. Line traces (mean±s.e.m) indicate the average distance in visual angle between gaze and the center of the tile clicked for match (green) and mismatch (black) trials. Reaction times (RT) and distances between the 1st and 2nd tiles were equalized (mean RT ± 200ms; mean distance ± 3°). **A**. No significant difference in eye-movements between match and mismatch was found during clicking the 1st tile. **B**. No significant difference in eye movements between match and mismatch was found before clicking the 2nd tile. Participants' gaze moved faster away from the 2nd tile in match trials than mismatch trials after the click: within the 1 second window after time zero, the distance from the gaze to the center of the tile was on average 1.76 dva (degrees of visual angle) larger for match than mismatch trials.

Figure S2

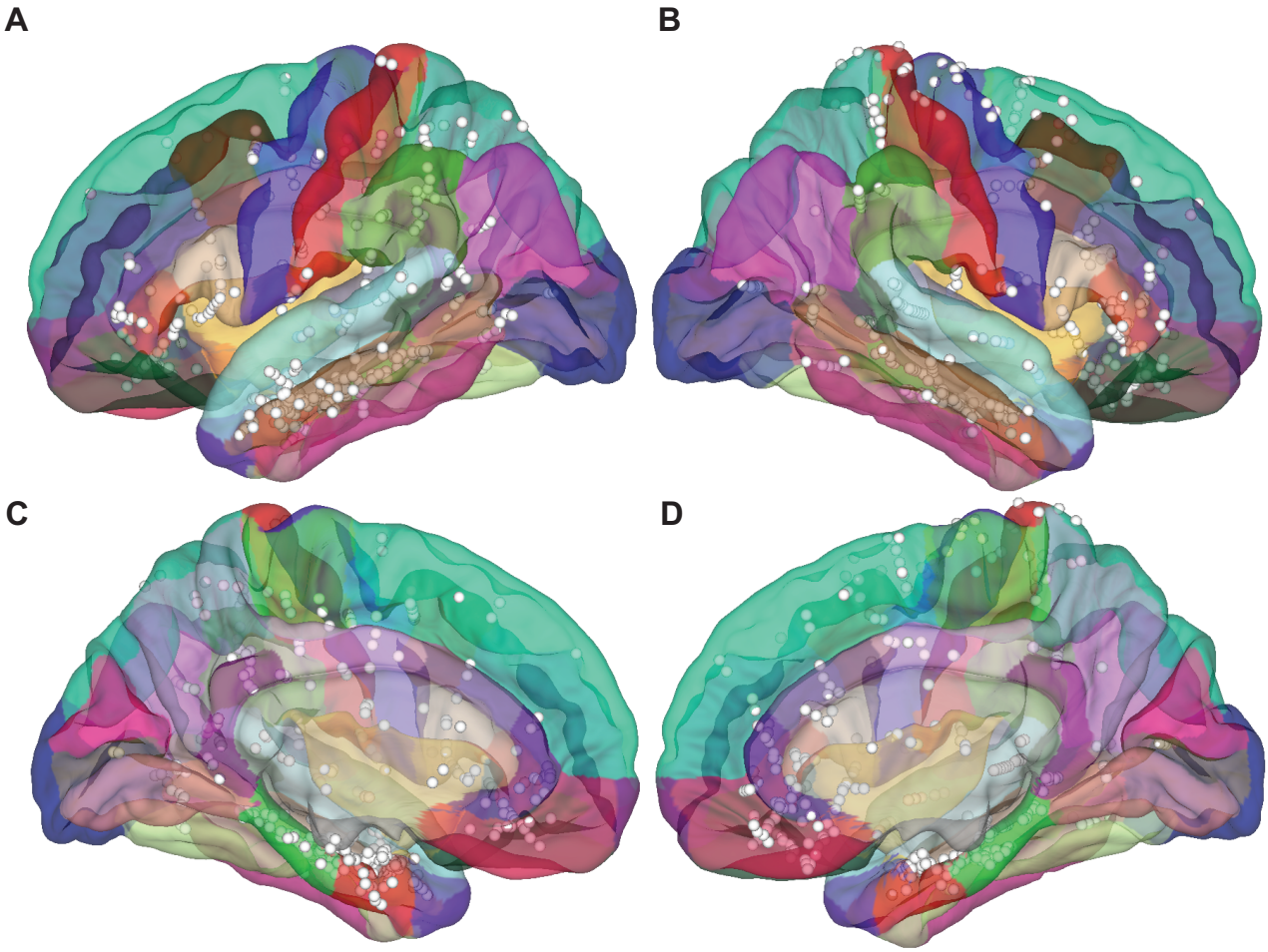

Figure S2. **Locations of electrodes in the gray matter**

Each circle shows a bipolarly referenced electrode (n=676), overlayed on the Desikan-Killiany Atlas with different views: **A**: left lateral; **B**: right lateral; **C**: left medial; **D**: right medial. The colors reflect the Desikan-Killiany parcellation (Desikan et al, 2006). Locations of white matter electrodes are reported in **Figure S3** (see also **Table S2**).

Figure S3

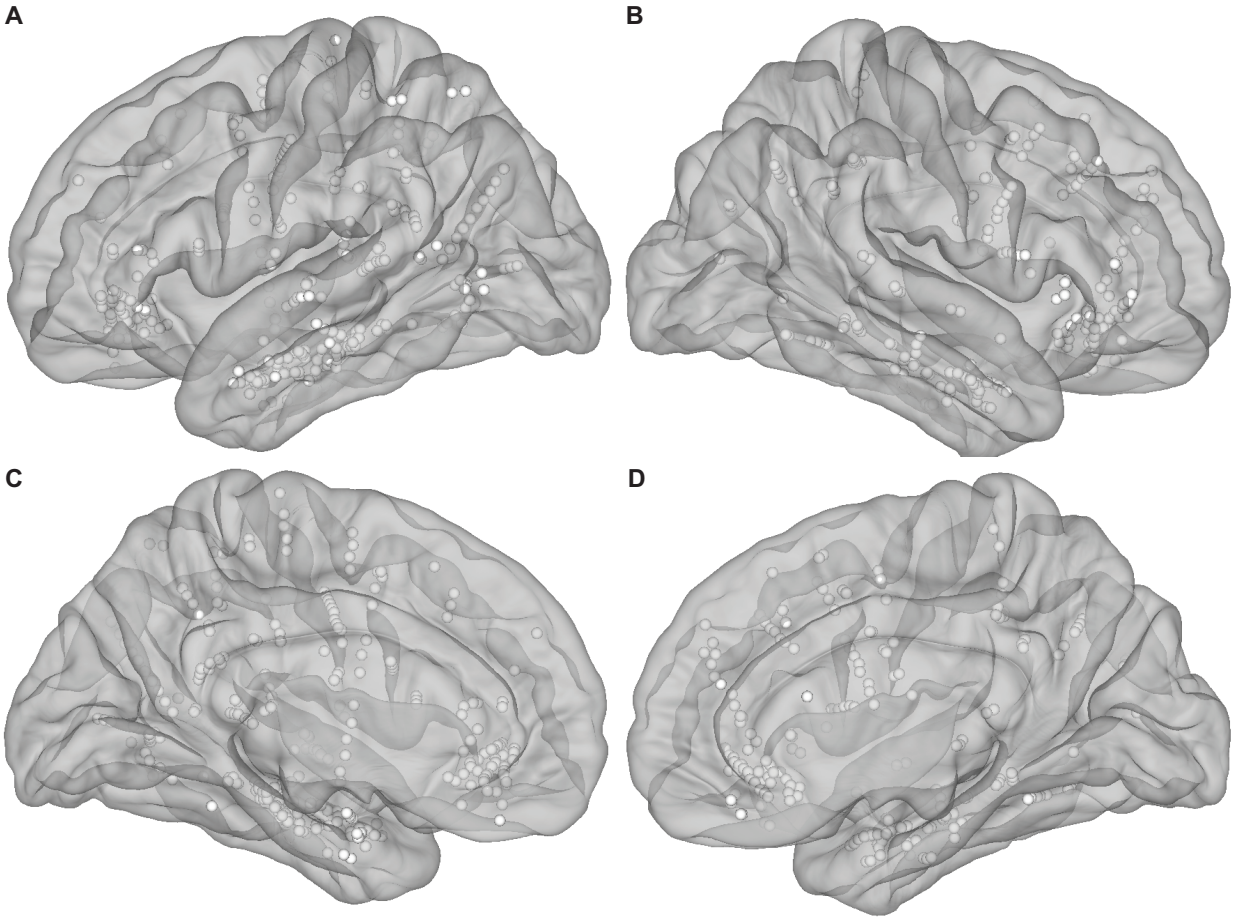

Figure S3. **Locations of all analyzed electrodes in the white matter.** Each sphere reflects one of each pair of nearby electrodes that were bipolarly referenced (n=492, **Table S2**). **A**: left lateral view; **B**: right lateral view; **C**: left medial view; **D**: right medial view. The location of gray matter electrodes is shown in **Figure S2**.

Figure S4

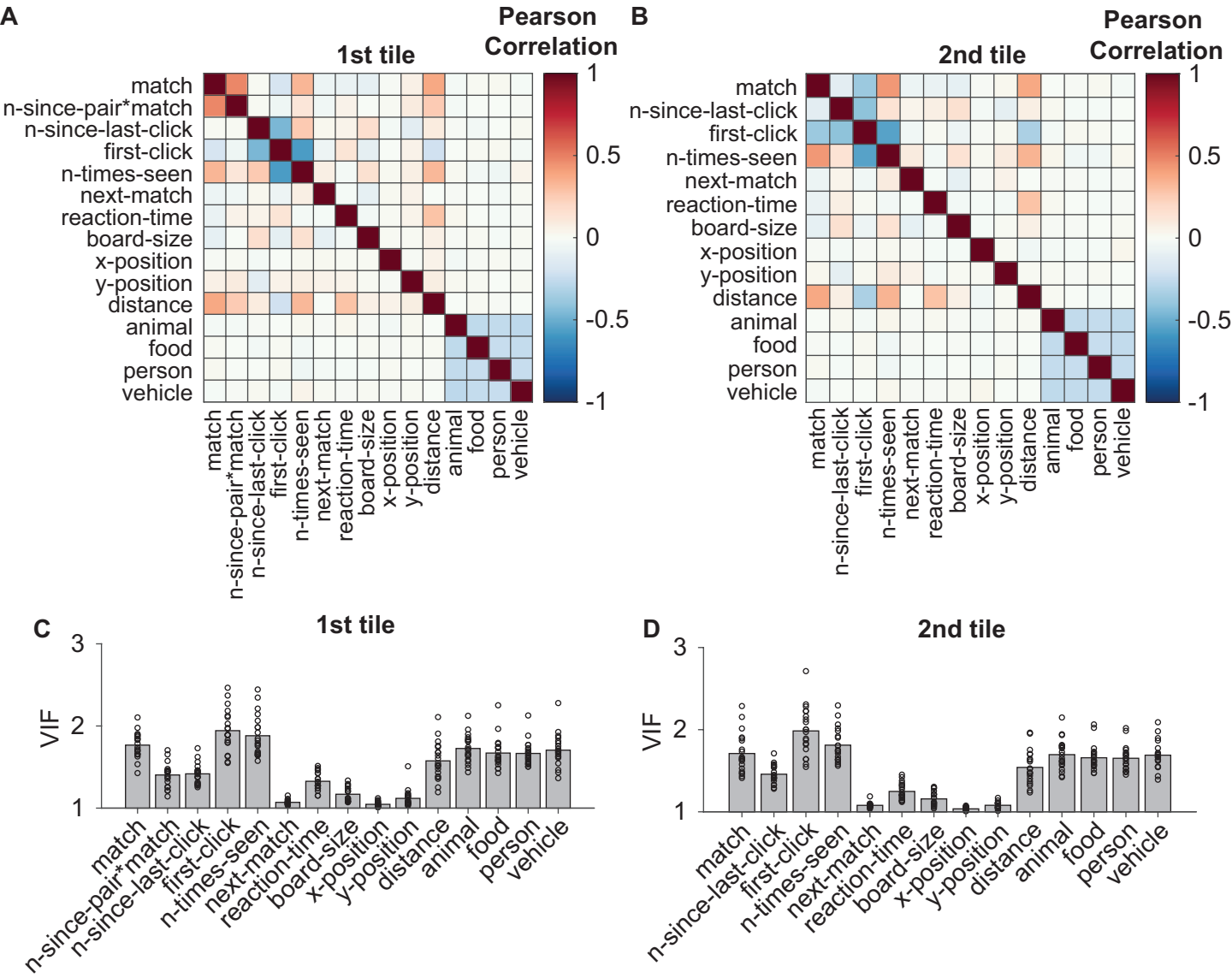

Figure S4. Correlation and collinearity among predictor variables.
A, **B**. Average across subjects of the Pearson correlation between pairs of predictors for the 1st tile (**A**) and the 2nd (**B**) tile. See color scale on the right. This is a symmetric matrix and the diagonal is 1, by definition. **Table 1** describes each of the predictors.
C, **D**. Variation Inflation Factor (VIF) (O'Brien, 2007) of each predictor for the 1st tile (**C**) and the 2nd (**D**) tile. Bar height indicates the average VIF of each predictor across all subjects. Dots represent the VIF of each predictor for each subject.

Figure S5

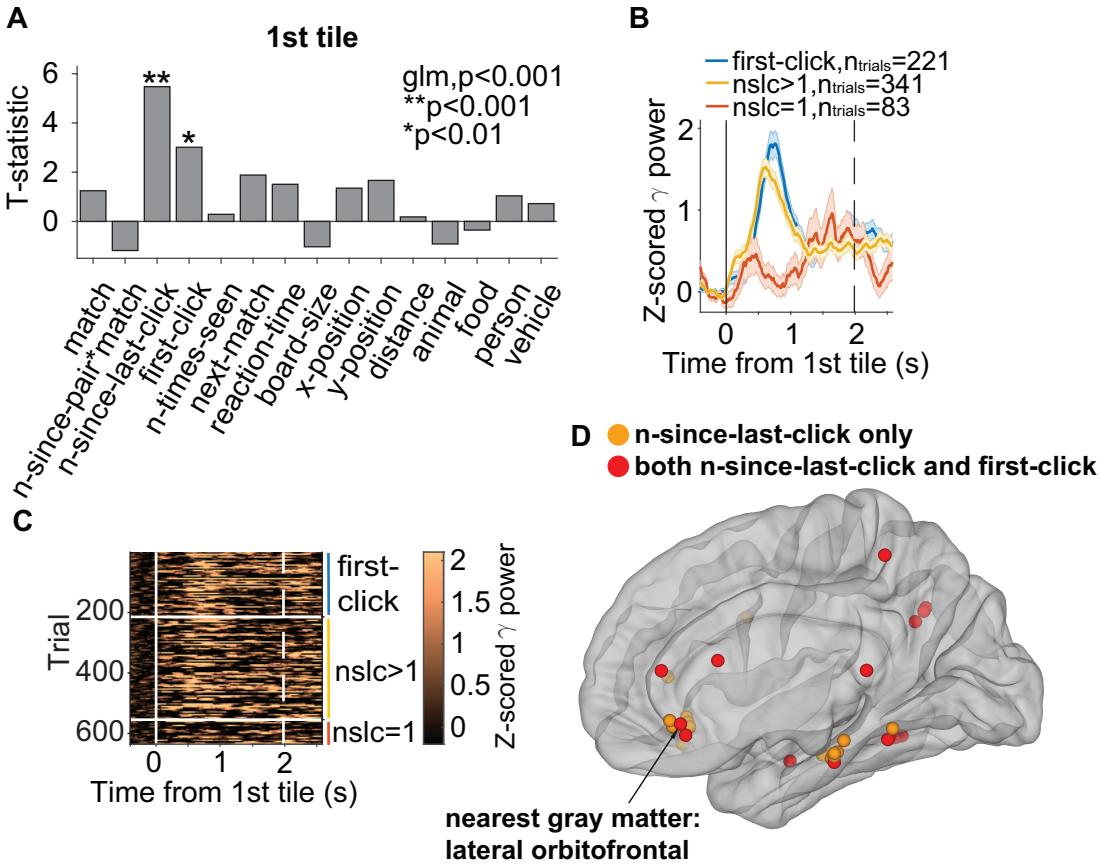

Figure S5. Neural signals in the white matter reflect novelty and familiarity

Panels show an example electrode in the white matter whose closest gray matter region is the left lateral orbitofrontal cortex (arrow in **D**). This figure follows the format of **Figure 3** in the main text.

A. T-statistic of each predictor in the GLM analysis (**Methods**). Asterisks indicate statistically significant predictors for the neural signals.

B. Z-scored gamma band power aligned to the 1st tile onset (solid vertical line) for novel tiles (blue), unfamiliar tiles (n-since-last-click>1, yellow), and more familiar tiles (n-since-last-click=1, red). The vertical dashed line indicates the mean reaction time. The time axis extends from 400 ms before the click to 500 ms after the average reaction time.

C. Raster plot showing the z-scored gamma power in individual trials ordered by first-click and then larger to smaller n-since-last-click; division indicated by white horizontal lines and colored vertical lines.

D. Locations of all white matter electrodes where n-since-last-click was a significant predictor during the 1st tile. Orange: n-since-last-click; red: both n-since-last-click and first-click were significant predictors. All electrodes were reflected on one hemisphere for display purposes.

Figure S6

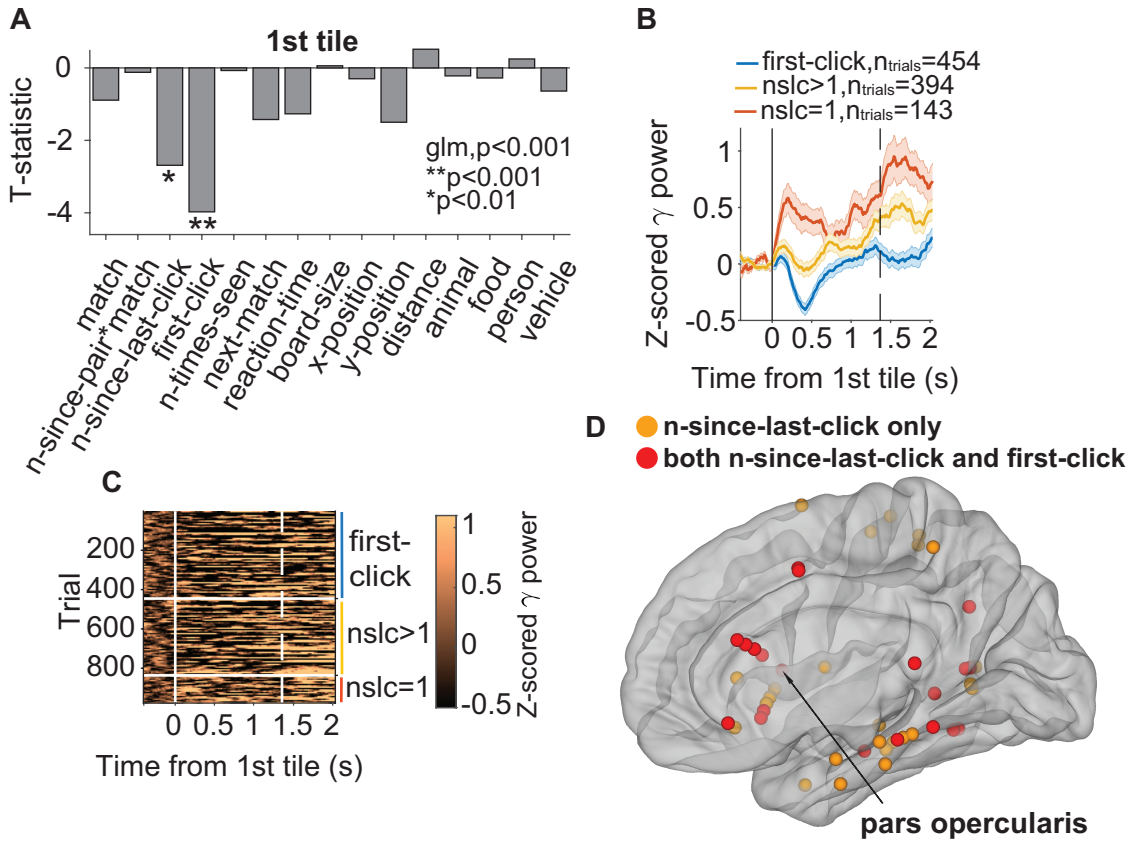

Figure S6. Neural signals reflect novelty and familiarity with a pattern different from that shown in Figure 3E-G.

This figure shows an example electrode in the right pars opercularis (gray matter, arrow in **D**), following the format of **Figure 3** in the main text. In contrast to **Figure 3E-G**, this electrode showed increased activity for more familiar trials.

A. T-statistic of each predictor in the GLM for the 1st tile. Asterisks indicate significant predictors for the gamma power AUC.

B. Z-scored gamma (30-150 Hz) power for first-click (blue), n-since-last-click>1 (yellow), and n-since-last-click=1 (red). Dashed line indicates the mean reaction time.

C. Raster plot showing the z-scored gamma power in individual trials ordered by first-click and then larger to smaller n-since-last-click; division indicated by white horizontal lines and colored vertical lines.

D. Locations of all n-since-last-click electrodes during the 1st tile. Orange: n-since-last-click only; red: both n-since-last-click and first-click were significant predictors. All electrodes were reflected on one hemisphere for display purposes.

Figure S7

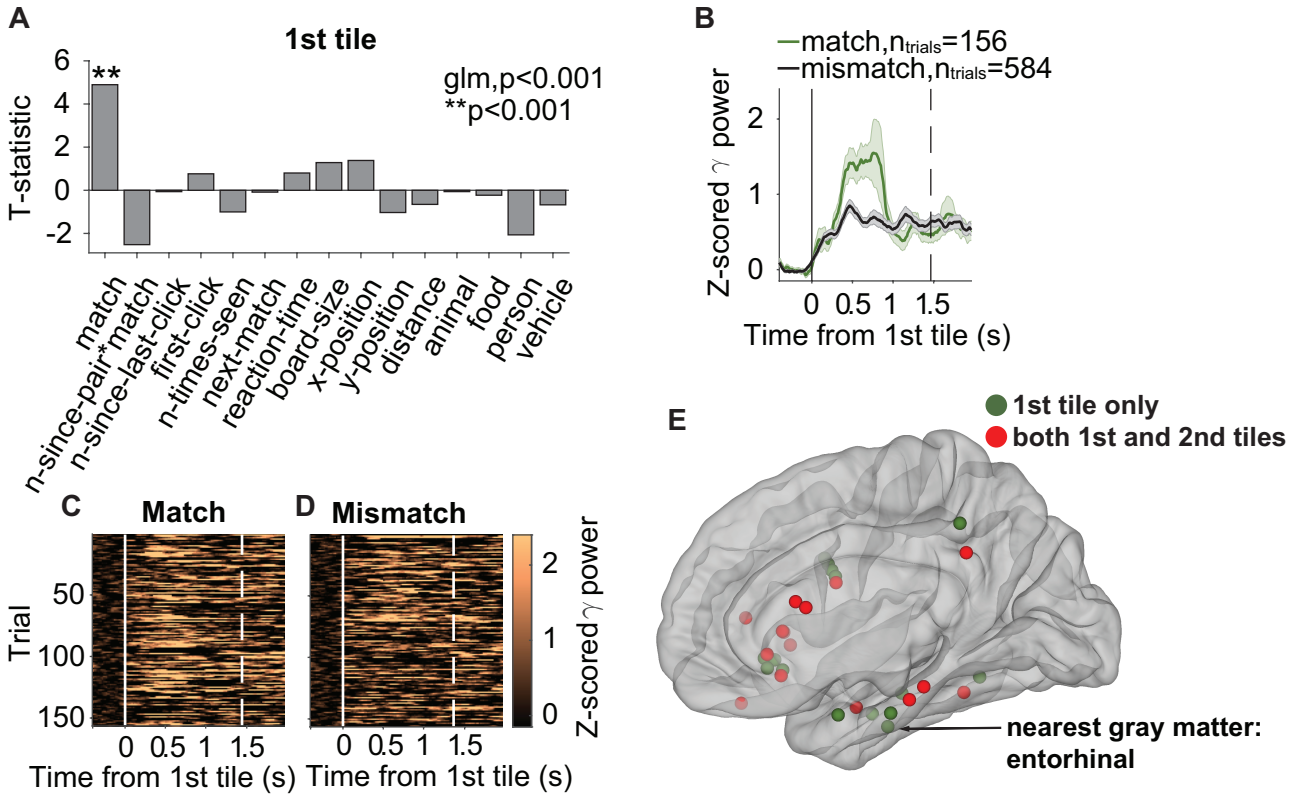

Figure S7. Neural signals in the white matter predict correct retrieval

Panels show an example electrode located in the white matter where the nearest gray matter region is the right entorhinal cortex (see arrow in **E**) as well as population locations in **E**. The format follows **Figure 3**.

A. t-statistic of each predictor in the GLM analysis. Asterisks indicate statistically significant predictors for the neural signals.

B. Z-scored gamma band power aligned to the 1st tile onset (solid vertical line) for match trials (green) and mismatch trials (black). The vertical dashed line indicates the mean reaction time. Shaded error bars indicate s.e.m.

C-D. Raster plots showing the gamma power in individual trials for match (**C**) and mismatch (**D**) trials.

E. Locations of all the white matter electrodes where match was a significant predictor during the 1st tile only (green) and during both tiles (red). All electrodes were reflected on one hemisphere for display purposes.

Figure S8

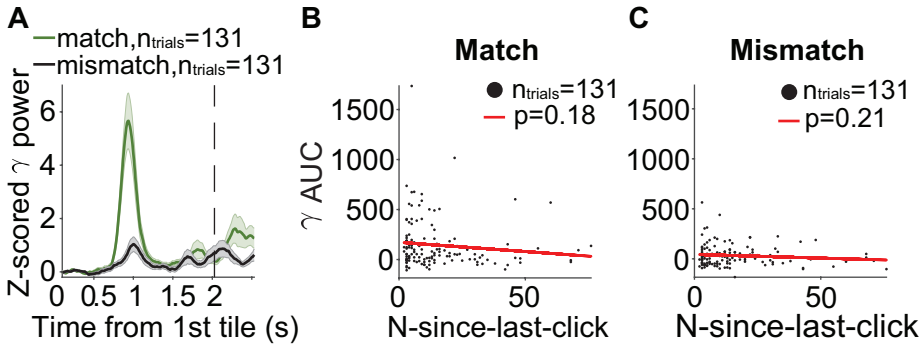

Figure S8. Match is the only predictor that accounts for the neural differences between match and mismatch

Panels shown the neural responses of an example electrode in the right lateral orbitofrontal cortex (same as in **Figure 4**) when equalizing the distribution of n-since-last click in match and mismatch trials.

A. Z-scored gamma (30-150 Hz) power during match (green) and mismatch (black) trials aligned to the 1st tile onset (solid line) after equalizing n-since-last-click values of match and mismatch trials by random subsampling. Dashed line indicates the mean reaction time.

B-C. Scatter plots of AUC of gamma power versus n-since-last-click for match (**B**) and mismatch (**C**) trials. Each dot represents data from one trial. Red lines represent linear fits of the data.

Figure S9

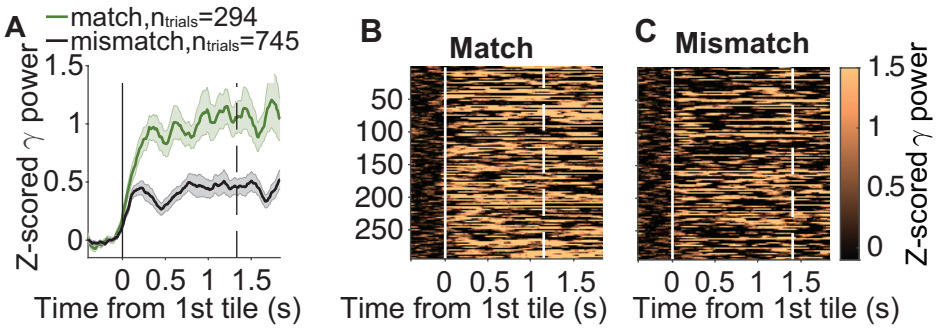

Figure S9. Neural signals predict correct retrieval with a pattern different from that shown in Figure 4

Panels show an example electrode located in the left middle temporal gyrus where "match" was a significant predictor for gamma activity.

A. Z-scored gamma (30-150 Hz) power during match (green) and mismatch (black) trials aligned to the 1st tile onset (solid line). Dashed line indicates the mean reaction time.

B-**C**. Raster plots showing the z-scored gamma power in individual match (**B**) and mismatch (**C**) trials. For display purposes, trial numbers of match and mismatch were equalized (**Methods**).

Figure S10

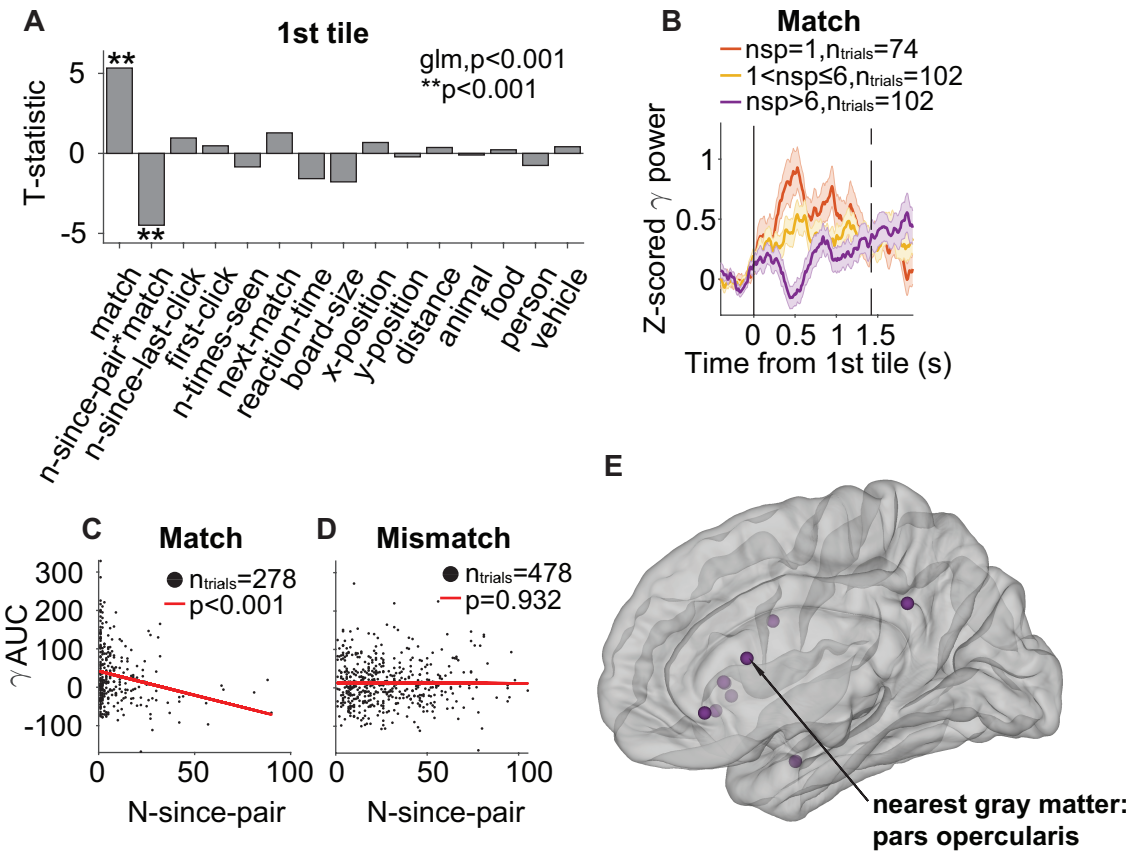

Figure S10. Neural signals in the white matter reflect the strength of memory retrieval
Panels show an example electrode in the white matter where the closest gray matter region is the left pars opercularis (see arrow in part **E**) and population locations in **E**.

A. T-statistic of each predictor in the GLM analysis. Asterisks indicate significant predictors for the neural signals.

B. Z-scored gamma band power aligned to the 1st tile onset (solid vertical line) for match trials with small n-since-pair (red, stronger memories), intermediate nsp (yellow), and large nsp (purple, weaker memories). The vertical dashed line indicates the mean reaction time. Shaded error bars indicate s.e.m.

C-D. Scatter plots of the area under the curve (AUC) of the gamma band power as a function of nsp for match trials (**C**) and mismatch trials (**D**). Each dot represents one trial. Red lines show linear fits to the data.

E. Locations of all white matter electrodes where nsp was a significant predictor. All electrodes were reflected on one hemisphere for display purposes.

Figure S11

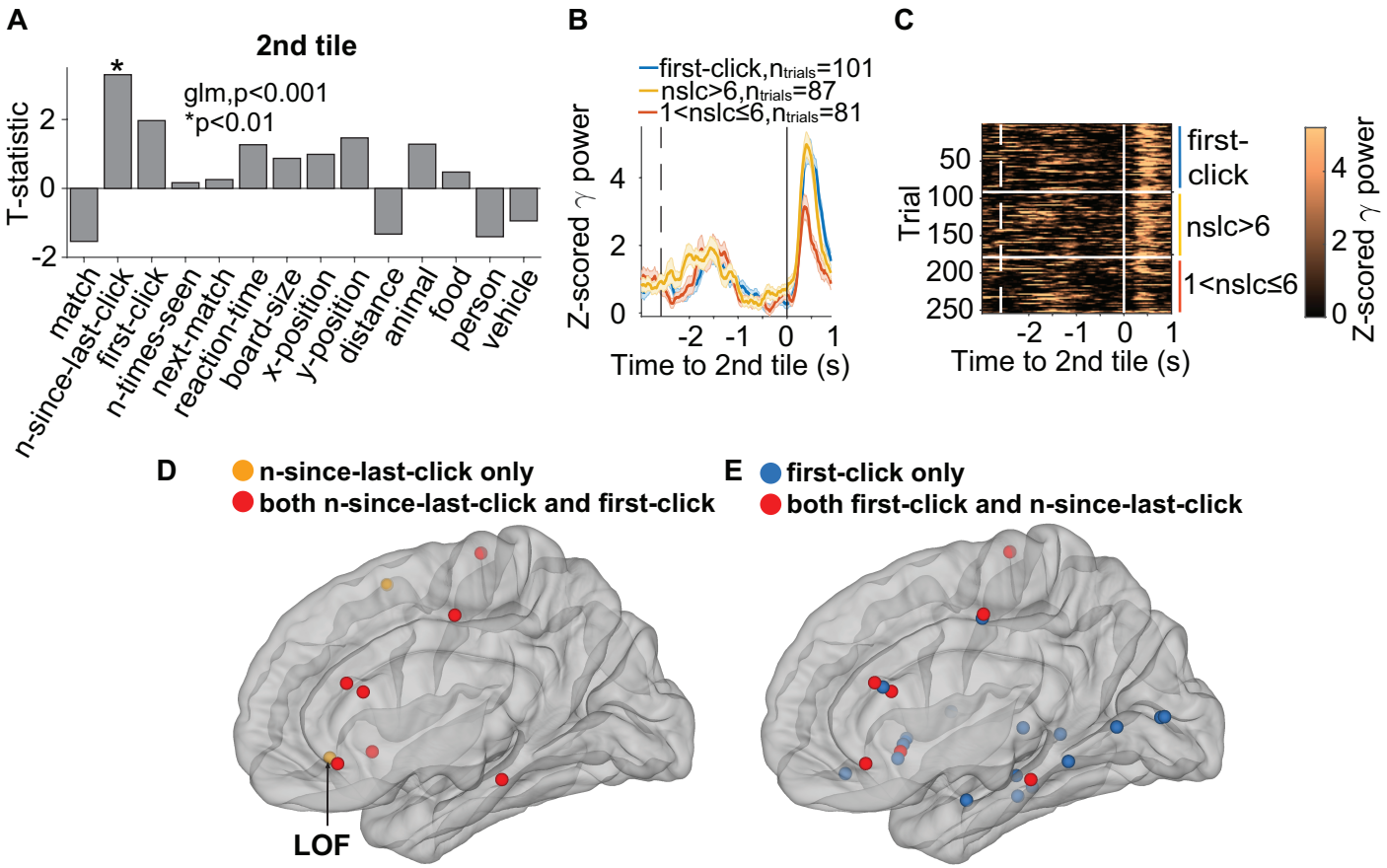

Figure S11. Neural signals after the second tile reflect familiarity and novelty
Panels show an example electrode in the right lateral orbitofrontal (LOF) cortex and population locations in **D**-**E**.

A. T-statistic of each predictor in the GLM analysis (**Methods**). Asterisks indicate statistically significant predictors for the neural signals.

B. Z-scored gamma band power aligned to the 2nd tile onset (solid vertical line) for novel tiles (blue), unfamiliar tiles (n-since-last-click>6, yellow), and familiar tiles (n-since-last-click≤1, red). The vertical dashed line indicates the mean onset of the 1st tile. The time axis extends from 400 ms plus the average reaction time before the click to 1,000 ms after the click.

C. Raster plots showing the z-scored gamma power in individual trials ordered by first-click and then larger to smaller n-since-last-click; division indicated by white horizontal lines/spaces and colored vertical bars.

D. Locations of all electrodes where n-since-last-click was a significant predictor during the 2nd tile. Orange: n-since-last-click only; red: both n-since-last-click and first-click were significant predictors.

E. Locations of all electrodes where first-click was a significant predictor during the 2nd tile. Blue: first-click only; red: both first-click and n-since-last-click were significant predictors. All electrodes were reflected on one hemisphere for display purposes.

Figure S12

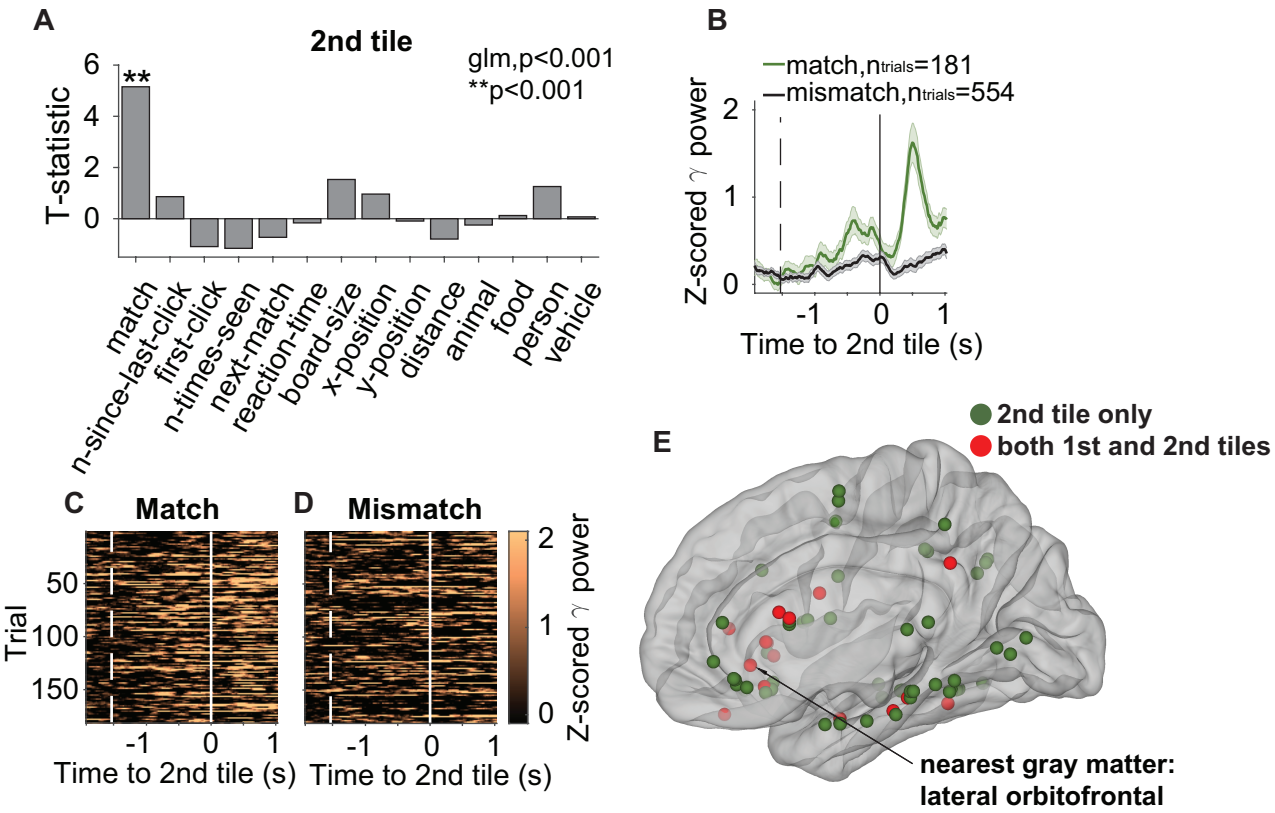

Figure S12. Neural signals in the white matter after the second tile reflect correct retrieval

Panels show an example electrode located in the white matter whose closest gray matter region is the right LOF (see arrow in part **E**).

A. T-statistic of each predictor in the GLM analysis for the responses after the 2nd tile. Asterisks indicate statistically significant predictors of neural signals.

B. Z-scored gamma band power aligned to the onset of the 2nd tile (solid vertical line) for match (green) and mismatch (black) trials. The dashed line indicates the mean onset of the 1st tile.

C-D. Raster plots showing the gamma band power in individual trials for match (left) and mismatch (right) trials.

E. Locations of all the white matter electrodes where match was a significant predictor during the 2nd tile only (green) and during both tiles (red). All electrodes were reflected on one hemisphere for display purposes.

Figure S13

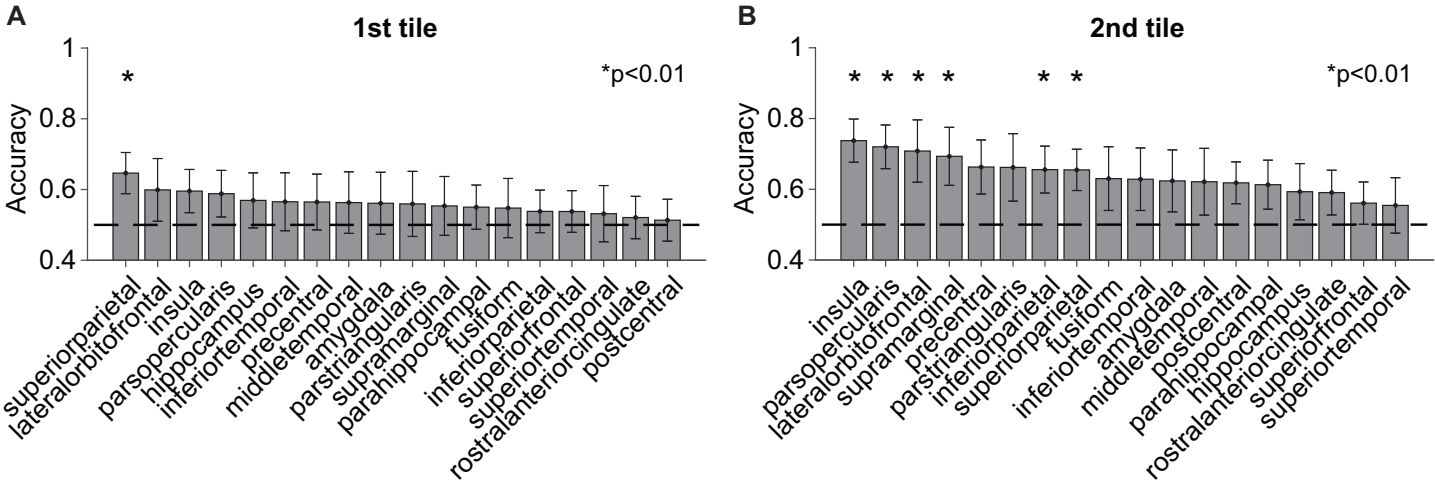

Figure S13. Decoding of match versus mismatch with random subsampling of 12 channels in each brain region.

Average decoding accuracy of each brain region (**Methods**) using neural responses after the 1st tile (**A**) and the 2nd tile (**B)**. The format follows **Figure 7**. Brain regions are ordered from higher to lower average decoding accuracy. Dashed horizontal lines indicate chance accuracy. Asterisks denote significant decoding accuracy above chance (α=0.01). All error bars indicate SD (n=1,000 iterations).

Table 1. Predictors in the generalized linear models, their definitions, and applicable tiles.

Predictor	Description	Which tile
match	Whether the trial was a match or mismatch	both
n-since-pair*match	how many clicks ago the tile's pair was clicked (matched trials only)	1st
n-since-last-click	how many clicks ago the same tile was clicked	both
first-click	Whether a tile was clicked the very first time	both
n-times-seen	number of times the same image had been previously clicked	both
next-match	whether the next trial was a match or mismatch	both
reaction-time	time between the 1st and 2nd tile	both
board-size	Total number of tiles in the current block	both
x-position	x position in pixel	both
y-position	y position in pixel	both
distance	distance between the 2nd tile of the current trial and the 1st tile of the next trial in pixel	both
animal	image belonged to animal category	both
food	image belonged to food category	both
person	image belonged to person category	both
vehicle	image belonged to vehicle category	both

Table S1: Information about each participant: hospital where data were recorded, gender, age, total number of electrodes implanted, number of electrodes analyzed in the gray matter, and number of electrodes analyzed in the white matter. All participants were right-handed.

Subject No.	Hospital	Gender	Age	# electrodes	# gray matter electrodes analyzed	# white matter electrodes analyzed
1	Xuanwu	female	22	85	37	21
2	Xuanwu	male	32	53	21	11
3	Xuanwu	male	19	114	32	68
4	Xuanwu	male	33	61	22	21
5	Xuanwu	male	35	71	28	27
6	Xuanwu	male	21	83	34	28
7	Xuanwu	male	26	86	34	35
8	Xuanwu	male	23	78	23	15
9	Xuanwu	female	47	34	11	4
10	Xuanwu	female	21	61	35	12
11	Xuanwu	female	26	78	17	9
12	BWH	female	32	51	29	0
13	BWH	female	31	74	24	19
14	BWH	female	26	60	15	15
15	BWH	male	22	104	30	21
16	BWH	female	52	98	35	28
17	BWH	male	44	58	20	9
18	BCH	male	18	154	85	26
19	BCH	female	12	188	97	46
20	BCH	male	15	159	47	77

Table S2: Distribution of electrode locations per hemisphere and brain region for the gray matter (left) and white matter (right). The location of any white matter electrode was based on its nearest gray matter region.

Gray matter				White matter (closest gray matter)			
Region	**Left**	**Right**	**Total**	**Region**	**Left**	**Right**	**Total**
amygdala	21	24	45	amygdala	0	0	0
bankssts	0	7	7	bankssts	5	2	7
caudalanteriorcingulate	1	3	4	caudalanteriorcingulate	1	0	1
caudalmiddlefrontal	1	5	6	caudalmiddlefrontal	1	7	8
entorhinal	5	0	5	cuneus	1	1	2
fusiform	15	10	25	entorhinal	2	2	4
hippocampus	36	31	67	fusiform	21	14	35
inferiorparietal	11	8	19	inferiorparietal	7	3	10
inferiortemporal	14	9	23	inferiortemporal	31	16	47
insula	13	15	28	insula	11	12	23
isthmuscingulate	6	0	6	isthmuscingulate	1	0	1
lateraloccipital	3	2	5	lateraloccipital	2	3	5
lateralorbitofrontal	19	32	51	lateralorbitofrontal	23	30	53
lingual	3	2	5	lingual	2	2	4
medialorbitofrontal	4	7	11	medialorbitofrontal	6	8	14
middletemporal	53	38	91	middletemporal	31	21	52
paracentral	4	0	4	paracentral	3	3	6
parahippocampal	10	13	23	parahippocampal	6	5	11
parsopercularis	11	5	16	parsopercularis	5	3	8
parsorbitalis	2	3	5	parsorbitalis	4	7	11
parstriangularis	13	19	32	parstriangularis	10	10	20
pericalcarine	0	1	1	pericalcarine	4	0	4
postcentral	8	12	20	postcentral	6	0	6
posteriorcingulate	4	3	7	posteriorcingulate	10	1	11
precentral	8	21	29	precentral	11	15	26
precuneus	3	0	3	precuneus	12	3	15
rostralanteriorcingulate	7	7	14	rostralanteriorcingulate	3	3	6
rostralmiddlefrontal	1	4	5	rostralmiddlefrontal	2	7	9
superiorfrontal	13	19	32	superiorfrontal	10	18	28
superiorparietal	8	12	20	superiorparietal	10	7	17
superiortemporal	26	21	47	superiortemporal	21	13	34
supramarginal	10	4	14	supramarginal	4	4	8
transversetemporal	6	0	6	transversetemporal	6	0	6
Total	**339**	**337**	**676**	**Total**	**272**	**220**	**492**

Table S3A. First tile GLM analysis for all gray matter electrodes that showed first-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow rows indicate the example electrodes in **Figure 4** (first and second rows) and **Figure S4** (third row)**.** *: $p<0.01$. **: $p<0.001$. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
Amygdala	7	3				* X											
Amygdala	15	81				*										** X	
bankssts	18	131				** X											
caudalmiddlefrontal	12	43				** X											
fusiform	1	42				*				*							** X
fusiform	3	11			*	*			**					** X			
fusiform	6	11			** X	*											*
fusiform	8	63			**	** X											
fusiform	16	92				* X											
inferiorparietal	3	71			** X	**			**							*	
inferiorparietal	18	150			** X	**				**		*					
inferiorparietal	18	151			** X	**					*					*	
inferiortemporal	18	143	*		**	** X											
inferiortemporal	18	144			** X	*											
insula	3	50				* X											
lateraloccipital	20	5				**			** X		*			*		*	
lateralorbitofrontal	3	40				** X			**	*			*				
lateralorbitofrontal	14	32				* X	*										
lateralorbitofrontal	15	22			** X	**		*	*			*					
lateralorbitofrontal	18	5				**				** X							
lateralorbitofrontal	18	6		*		** X				**							
lateralorbitofrontal	18	7				** X				*							
lateralorbitofrontal	18	20				** X	*										
lateralorbitofrontal	18	21				** X											
lateralorbitofrontal	18	22				** X											
lateralorbitofrontal	18	25	*		*	* X				*							
lateralorbitofrontal	18	26	**	**	**	** X				*							
lateralorbitofrontal	19	41				* X											
medialorbitofrontal	18	18				* X				*							
medialorbitofrontal	18	19				** X											
middletemporal	18	108				** X											
middletemporal	18	110	** X	*		*										*	
middletemporal	18	134			*	* X											
middletemporal	18	148				** X											
parahippocampal	9	27				* X											
parsopercularis	8	22			** X	**			**					*			
parsopercularis	8	23			**	** X			**							**	
parsopercularis	11	78			*	** X		*						*			*
parsopercularis	18	30				** X											
parsopercularis	18	32			*	** X											
parstriangularis	18	11				*				*				* X		*	
parstriangularis	18	13				**							** X				
parstriangularis	18	14				** X							*				
precentral	15	15			*	** X			**								
precentral	15	16			**	** X				**							
precentral	18	38				** X											
precentral	12	42				** X											
rostralmiddlefrontal	8	24			**	** X			**							*	
superiortemporal	2	44			*	** X											
supramarginal	2	32	** X	**		*	**		**				*				

Table S3B. First tile GLM analysis for all white matter electrodes that showed first-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure S4**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**		** X	**			**								
fusiform	3	28			** X	**			**				*			**	
fusiform	18	106				* X											
fusiform	18	138			**	** X				**	**					*	
fusiform	18	139			**	** X				*	*						
fusiform	18	140			**	** X			**	**	*						
fusiform	18	141			**	** X				*							
fusiform	18	142	*		**	** X				*							
inferiortemporal	1	43				*											** X
inferiortemporal	1	69				* X		*									
inferiortemporal	1	82				** X		*									
inferiortemporal	6	58				** X	**										
inferiortemporal	7	39			**	*			** X		*						
inferiortemporal	18	107				** X											
lateralorbitofrontal	15	21			** X	**			*								
lateralorbitofrontal	15	23			** X	*											
lateralorbitofrontal	18	4				** X											
lateralorbitofrontal	18	10				** X											
lateralorbitofrontal	18	23				** X											
lateralorbitofrontal	18	24				** X											
parahippocampal	1	10				*			*					** X	**	**	*
parsopercularis	18	31				** X		*									
parstriangularis	16	8				** X							*				
rostralmiddlefrontal	3	80				** X											
rostralmiddlefrontal	15	3			** X	**											
superiorfrontal	15	10				*			** X								
superiorparietal	3	20	*			*				* X							
superiorparietal	3	23			** X	**			*								
superiorparietal	3	70			** X	**											
superiorparietal	3	72			** X	**			*								
superiorparietal	3	73			** X	**			**		*						
superiortemporal	2	40				* X											
superiortemporal	2	43			**	** X											**

Table S4A. First tile GLM analysis for all gray matter electrodes that showed n-since-last-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow rows indicate the example electrodes in **Figure 4E-H** (first row) and **Figure S5** (second row).*: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
Hippocampus	6	6			*		* X										
bankssts	16	41			*									*		** X	
bankssts	16	42			*									*	*	** X	
entorhinal	6	27	*		* X												
fusiform	2	13			* X												
fusiform	3	11			*	*			**					** X			
fusiform	6	11			** X	*											*
fusiform	8	63			**	** X											
inferiorparietal	3	71			** X	**			**							*	
inferiorparietal	18	150			** X	**				**		*					
inferiorparietal	18	151			** X	**					*					*	
inferiorparietal	18	152			** X												
inferiortemporal	7	38	*		*				** X		*						
inferiortemporal	18	143	*		**	** X											
inferiortemporal	18	144			** X	*											
insula	18	27	**	**	** X												
insula	18	28	**	**	** X												
insula	18	29	**	**	** X												
insula	18	34			**					** X							
lateralorbitofrontal	15	22			** X	**		*	*			*					
lateralorbitofrontal	15	73			*				**							** X	
lateralorbitofrontal	18	25	*		*	* X				*							
lateralorbitofrontal	18	26	**	**	**	** X				*							
middletemporal	11	45		*	* X			*									
middletemporal	14	48			* X												
middletemporal	16	24			*				*					** X			
middletemporal	18	134			*	* X											
parahippocampal	6	8			**												** X
parahippocampal	6	9			**							**					** X
parahippocampal	10	8			* X												
parsopercularis	8	22			** X	**			**					*			
parsopercularis	8	23			**	** X			**							**	
parsopercularis	11	78			*	** X		*						*			*
parsopercularis	18	32			*	** X											
parstriangularis	10	59			** X												
postcentral	12	39			*				* X			*					
postcentral	12	49			** X												
precentral	15	15			*	** X			**								
precentral	15	16			**	** X				**							
rostralmiddlefrontal	8	24			**	** X			**							*	
superiorfrontal	12	6			**				** X								
superiorparietal	3	111			*				*		** X						
superiorparietal	3	112			*				* X								
superiortemporal	2	44			*	** X											
supramarginal	2	37			*				** X				**				

Table S4B. First tile GLM analysis for all white matter electrodes that showed n-since-last-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **FigureS4**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**		** X	**			**								
fusiform	3	12			**				**					** X		**	
fusiform	3	28			** X	**			**				*			**	
fusiform	6	12			*					*				** X	*	**	
fusiform	6	53			** X											**	**
fusiform	18	138			**	** X				**	**					*	
fusiform	18	139			**	** X				*	*						
fusiform	18	140			**	** X			**	**	*						
fusiform	18	141			**	** X				*							
fusiform	18	142	*		**	** X				*							
inferiortemporal	7	39			**	*			** X		*						
inferiortemporal	7	40			*										**	** X	
inferiortemporal	7	41			*				**					** X	**	**	
lateralorbitofrontal	6	66			* X												
lateralorbitofrontal	6	67			**				** X								
lateralorbitofrontal	6	68			*												** X
lateralorbitofrontal	13	31			* X				*								
lateralorbitofrontal	15	21			** X	**			*								
lateralorbitofrontal	15	23			** X	*											
lateralorbitofrontal	15	74	*		**										*	** X	
lateralorbitofrontal	15	75			* X												
middletemporal	5	66			* X												
parahippocampal	6	50	*		** X												
parsorbitalis	15	76	** X		*												
parstriangularis	4	49	** X		*				*								
precentral	4	59	* X		*												
rostralmiddlefrontal	15	3			** X	**											
superiorparietal	3	23			** X	**			*								
superiorparietal	3	70			** X	**											
superiorparietal	3	72			** X	**			*								
superiorparietal	3	73			** X	**			**		*						
superiortemporal	2	43			**	** X											**

Table S5A. First tile GLM analysis for all gray matter electrodes that showed match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow rows indicate the example electrodes in **Figure 5** (first row), **Figure S7** (first row), and **Figure S8** (second row).*: p<0.01. **: p<0.001. X: most significant predictor.

Region	Subject	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
Hippocampus	2	47	* X														
Hippocampus	16	28	** X														
bankssts	4	36	* X												*		
entorhinal	6	27	*		* X												
fusiform	6	10	*														* X
inferiortemporal	7	18	** X														
inferiortemporal	7	38	*		*				** X		*						
inferiortemporal	18	143	*		**	** X											
insula	18	27	**	**	** X												
insula	18	28	**	**	** X												
insula	18	29	**	**	** X												
insula	19	55	* X														
lateralorbitofrontal	4	39	* X											*			
lateralorbitofrontal	4	42	* X														
lateralorbitofrontal	4	43	** X														
lateralorbitofrontal	4	45	** X								*						
lateralorbitofrontal	10	46	** X														
lateralorbitofrontal	18	25	*		*	* X				*							
lateralorbitofrontal	18	26	**	**	**	** X				*							
middletemporal	2	52	** X	**													
middletemporal	8	37	*				*									** X	
middletemporal	13	45	**						*			*	** X				
middletemporal	18	109	* X														
middletemporal	18	110	** X	*		*										*	
parahippocampal	10	7	** X	*													
parsopercularis	6	82	** X					*	*								
parsopercularis	6	83	** X	*													
parsopercularis	10	57	** X							*							
precentral	19	106	** X	*												*	
precuneus	1	77	** X	*													
rostralanteriorcingulate	9	34	** X														
supramarginal	2	32	** X	**		*	**		**				*				

Table S5B. First tile GLM analysis for all white matter electrodes that showed match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure S6**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**		** X	**			**								
entorhinal	10	19	** X														
fusiform	18	142	*		**	** X				*							
inferiortemporal	6	57	** X														
inferiortemporal	7	19	* X														
inferiortemporal	7	63	* X														
lateralorbitofrontal	4	41	** X														
lateralorbitofrontal	4	44	* X														
lateralorbitofrontal	10	55	** X	**			*										
lateralorbitofrontal	14	34	** X														
lateralorbitofrontal	14	36	** X	*			*										*
lateralorbitofrontal	15	74	*		**										*	** X	
lingual	11	60	*								**	*		**		** X	
medialorbitofrontal	11	63	** X					*									
middletemporal	9	24	** X														
middletemporal	13	44	*						*			*	** X				
parahippocampal	6	50	*		** X												
parsopercularis	6	81	** X	**													
parsorbitalis	15	76	** X		*												
parstriangularis	4	49	** X		*				*								
parstriangularis	7	82	** X	*													
parstriangularis	7	84	** X	**													
precentral	4	55	** X														
precentral	4	56	** X														
precentral	4	57	** X	*													
precentral	4	58	** X														
precentral	4	59	* X		*												
superiorparietal	3	20	*			*				* X							
superiortemporal	6	19	*					*			* X		*				
supramarginal	2	31	** X	**					*								

Table S6A. First tile GLM analysis for all gray matter electrodes that showed n-since-pair*match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure 6**.*: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
insula	18	27	**	**	** X												
insula	18	28	**	**	** X												
insula	18	29	**	**	** X												
lateralorbitofrontal	18	3		* X													
lateralorbitofrontal	18	6		*		** X				**							
lateralorbitofrontal	18	26	**	**	**	** X				*							
medialorbitofrontal	18	2		* X													
middletemporal	2	52	** X	**													
middletemporal	11	45		*	* X			*									
middletemporal	18	110	** X	*		*										*	
parahippocampal	10	7	** X	*													
parsopercularis	6	83	** X	*													
precentral	19	106	** X	*												*	
precuneus	1	77	** X	*													
supramarginal	2	32	** X	**		*	**		**				*				

Table S6B. First tile GLM analysis for all white matter electrodes that showed n-since-pair*match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure S9**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-pair* match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
lateralorbitofrontal	10	55	** X	**			*										
lateralorbitofrontal	14	6		** X									*				
lateralorbitofrontal	14	36	** X	*			*										*
middletemporal	18	60		*						* X		*					
parsopercularis	6	81	** X	**													
parstriangularis	7	82	** X	*													
parstriangularis	7	84	** X	**													
precentral	4	57	** X	*													
supramarginal	2	31	** X	**					*								

Table S7A. Second tile GLM analysis for all gray matter electrodes that showed first-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
Amygdala	10	10			* X											
Hippocampus	18	104	** X		**											
bankssts	18	131	*		*			** X	*							
fusiform	3	11		*	*								** X			
fusiform	10	37			*											** X
insula	18	27	** X		**	*		*								
insula	18	28	** X		*	*										
lateraloccipital	20	4			* X											
lateraloccipital	20	5			** X											
lateralorbitofrontal	15	22	*	**	**		*							**		** X
lateralorbitofrontal	18	5			* X				*							
lateralorbitofrontal	18	25	**		** X	**		**								
lateralorbitofrontal	18	26	**	*	** X	**		**								
lingual	1	12	*		*						** X			*		
parahippocampal	9	27			*				** X							
parsopercularis	8	22	**	**	**			** X	**				**			
parsopercularis	8	23	**		**			** X	**							
postcentral	20	83			* X					*						
postcentral	20	84		*	* X											
precentral	18	40			* X	*						*				
precentral	12	24	*	*	* X											
precuneus	1	77			*		** X									
rostralmiddlefrontal	8	24	** X	*	**			**								
superiortemporal	18	119			* X						*					

Table S7B. Second tile GLM analysis for all white matter electrodes that showed first-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**	**	*			** X								
fusiform	18	138	** X	**	*				**	*					*	
inferiorparietal	20	15			** X											
lateralorbitofrontal	6	68		*	** X	*										
lateralorbitofrontal	15	23		*	**											** X
lateralorbitofrontal	18	24	**	*	** X	*										
parstriangularis	16	7			** X											
parstriangularis	16	9			** X											
posteriorcingulate	20	123			** X			*								
precentral	4	54			* X											
precentral	4	57			*		* X									
precentral	4	58			*		** X									

Table S8A. Second tile GLM analysis for all gray matter electrodes that showed n-since-last-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure S10**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
fusiform	3	11		*	*								** X			
lateralorbitofrontal	122	46		* X												
lateralorbitofrontal	15	22	*	**	**		*							**		** X
lateralorbitofrontal	18	9	** X	*				**	*							
lateralorbitofrontal	18	26	**	*	** X	**		**								
parsopercularis	8	22	**	**	**			** X	**				**			
postcentral	20	84		*	* X											
precentral	12	24	*	*	* X											
rostralmiddlefrontal	8	24	** X	*	**			**								

Table S8B. Second tile GLM analysis for all white matter electrodes that showed n-since-last-click as a significant predictor. Each column (starting from column 4) shows a separate predictor. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**	**	*			** X								
caudalmiddlefrontal	3	90		** X			*									
fusiform	3	28		**				*							** X	
fusiform	6	12	**	**									** X	*	*	
fusiform	6	53		*				**							** X	*
fusiform	18	138	** X	**	*				**	*					*	
fusiform	18	139	** X	**				*		*						
fusiform	18	140	** X	*				**		**						
fusiform	18	141	** X	**				**		*						
lateralorbitofrontal	6	68		*	** X	*										
lateralorbitofrontal	15	21	** X	*												
lateralorbitofrontal	15	23		*	**											** X
lateralorbitofrontal	15	74		*				** X							*	
lateralorbitofrontal	18	24	**	*	** X	*										
middletemporal	7	10		* X												
middletemporal	7	66		*										* X	*	
middletemporal	7	67	* X	*							*					
parahippocampal	6	50	*	** X												
parsorbitalis	6	71		* X												
parsorbitalis	15	76		*				*								** X
parstriangularis	2	28		* X												
parstriangularis	2	29		*												* X
parstriangularis	7	83	** X	*			*									
superiorparietal	3	72	** X	*					*						*	

Table S9A. Second tile GLM analysis for all gray matter electrodes that showed match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure 7** and **Figure S9**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
Amygdala	6	16	*				* X									
Amygdala	7	4	** X													
Amygdala	8	51	** X													
Hippocampus	2	47	* X			*										
Hippocampus	16	28	** X													
Hippocampus	18	102	** X													
Hippocampus	18	103	** X													
Hippocampus	18	104	** X		**											
Hippocampus	18	105	** X													
bankssts	16	42	*											* X		
bankssts	18	131	*		*			** X	*							
bankssts	18	132	** X					**	*							
caudalmiddlefrontal	13	69	** X							*						
caudalmiddlefrontal	13	73	** X													
entorhinal	19	2	*									* X				
inferiorparietal	3	60	** X						*							
inferiorparietal	3	71	** X					**					*		**	
inferiorparietal	16	62	** X						*							
inferiorparietal	16	63	** X													
inferiortemporal	1	65	* X													
inferiortemporal	1	66	*					*							*	* X
inferiortemporal	7	21	** X													
inferiortemporal	7	37	* X					*								
inferiortemporal	7	38	** X					**								
insula	3	50	** X													
insula	6	77	** X					*								
insula	7	79	** X													
insula	7	80	** X													
insula	18	27	** X		**	*		*								
insula	18	28	** X		*	*										
insula	18	29	** X													
insula	18	44	** X													
insula	18	45	** X													
insula	19	55	** X													
insula	19	104	* X					*								
insula	20	151	* X													
lateraloccipital	16	81	*					** X								
lateralorbitofrontal	4	39	** X													
lateralorbitofrontal	4	43	** X													
lateralorbitofrontal	4	45	** X													
lateralorbitofrontal	10	40	** X													
lateralorbitofrontal	10	43	** X													
lateralorbitofrontal	10	46	** X													

Table S9A continued...

lateralorbitofrontal	13	28	** X													
lateralorbitofrontal	13	29	** X				*									
lateralorbitofrontal	13	30	** X				**									
lateralorbitofrontal	15	22	*	**	**		*							**		** X
lateralorbitofrontal	18	3	** X					**			*					
lateralorbitofrontal	18	7	** X						**							
lateralorbitofrontal	18	8	** X					**	**							
lateralorbitofrontal	18	9	** X	*				**	*							
lateralorbitofrontal	18	20	** X						*							
lateralorbitofrontal	18	21	** X													
lateralorbitofrontal	18	22	** X											*		
lateralorbitofrontal	18	25	**		** X	**		**								
lateralorbitofrontal	18	26	**	*	** X	**		**								
lateralorbitofrontal	19	41	* X													
lateralorbitofrontal	19	54	* X													
lingual	1	12	*		*						** X			*		
medialorbitofrontal	18	2	** X					**	**							
medialorbitofrontal	18	18	** X													
medialorbitofrontal	18	19	** X						*							
middletemporal	1	60	** X								*					
middletemporal	2	52	** X													
middletemporal	9	32	** X													
middletemporal	13	19	* X													
middletemporal	13	45	** X													
middletemporal	16	22	* X													
middletemporal	16	23	* X													
middletemporal	16	24	* X													
middletemporal	18	108	** X													
middletemporal	18	109	** X													
middletemporal	18	133	** X						**		**					
middletemporal	18	134	** X								**					
middletemporal	18	135	** X						**		**					
middletemporal	18	148	* X													
parahippocampal	6	8	**										*	**	*	** X
parahippocampal	6	9	*										*			** X

Table S9A continued ...

parsopercularis	6	78	** X					*		**		**				
parsopercularis	8	22	**	**	**			** X	**				**			
parsopercularis	8	23	**		**			** X	**							
parsopercularis	18	30	** X			*			*							
parsopercularis	18	32	**					** X	*							
parsopercularis	20	50	* X													
parstriangularis	2	25	** X													
parstriangularis	6	74	** X					**								
parstriangularis	6	75	** X					**								
parstriangularis	10	59	** X													
parstriangularis	18	11	* X													
parstriangularis	18	12	** X					**	*							
parstriangularis	18	13	** X									*				
parstriangularis	18	14	** X					**	*							
postcentral	18	35	** X													
postcentral	12	39	* X													
posteriorcingulate	20	73	* X			*										
precentral	122	32	* X			*										
precentral	122	33	** X													
precentral	15	16	** X							*						
precentral	16	50	** X													
precentral	16	53	** X													
precentral	18	36	** X										*			
precentral	12	24	*	*	* X											
rostralanteriorcingulate	9	34	** X													
rostralmiddlefrontal	8	24	** X	*	**			**								
superiorfrontal	19	175	** X					*								
superiorfrontal	12	6	*					** X								
superiorparietal	16	61	** X					*	*							
superiorparietal	20	129	** X													
superiorparietal	20	130	** X													*
supramarginal	2	37	* X													
supramarginal	16	64	** X													
supramarginal	16	65	** X													

Table S9B. Second tile GLM analysis for all white matter electrodes that showed match as a significant predictor. Each column (starting from column 4) shows a separate predictor. Yellow row indicates the example electrode in **Figure S11**. *: p<0.01. **: p<0.001. X: most significant predictor.

Region	Sub	Channel	match	n-since-last-click	first-click	n-times-seen	next-match	RT	board-size	x-position	y-position	distance	animal	food	person	vehicle
caudalanteriorcingulate	8	21	**	**	*			** X								
fusiform	6	12	**	**									** X	*	*	
fusiform	7	5	** X													
fusiform	7	6	* X													
fusiform	18	106	** X													
fusiform	18	138	** X	**	*				**	*					*	
fusiform	18	139	** X	**				*		*						
fusiform	18	140	** X	*				**		**						
fusiform	18	141	** X	**				**		*						
inferiorparietal	3	59	** X													
inferiortemporal	1	69	** X				*					*				
inferiortemporal	1	81	** X													
inferiortemporal	6	42	** X				*	**								
inferiortemporal	6	57	** X													
inferiortemporal	6	58	** X													
inferiortemporal	6	59	* X													
inferiortemporal	6	60	*					* X								
inferiortemporal	7	39	** X					**								
inferiortemporal	18	107	** X													
inferiortemporal	18	147	* X						*							
insula	3	49	** X													
lateralorbitofrontal	4	40	** X													
lateralorbitofrontal	4	41	** X													
lateralorbitofrontal	4	44	** X													
lateralorbitofrontal	6	64	** X								*					
lateralorbitofrontal	6	66	** X													
lateralorbitofrontal	6	67	** X													
lateralorbitofrontal	10	55	** X				**									
lateralorbitofrontal	13	32	*					** X				*				
lateralorbitofrontal	15	21	** X	*												
lateralorbitofrontal	18	23	** X													
lateralorbitofrontal	18	24	**	*	** X	*										
lingual	11	60	*										** X	**	**	
medialorbitofrontal	11	63	** X													
middletemporal	5	9	* X													
middletemporal	7	65	*					*					*	* X		
middletemporal	7	67	* X	*							*					
middletemporal	13	44	** X													
paracentral	3	106	*					*	** X							
parahippocampal	1	10	**										** X	**	**	
parahippocampal	6	50	*	** X												
parsopercularis	6	79	** X									*				
parsopercularis	6	80	** X					*		*						
parsopercularis	6	81	** X					*								
parsopercularis	13	67	** X													
parsorbitalis	5	54	** X													
parstriangularis	4	49	* X													
parstriangularis	7	82	** X				*				*					
parstriangularis	7	83	** X	*			*									
parstriangularis	7	84	** X									*				
pericalcarine	20	1	* X													
precentral	3	54	* X				*									
precentral	3	55	** X				*						*	**		
precentral	4	55	** X					*								
rostralmiddlefrontal	3	80	* X													
rostralmiddlefrontal	15	3	** X													
superiorfrontal	19	173	** X													
superiorfrontal	19	174	** X													
superiorfrontal	19	183	** X													
superiorparietal	3	21	*					** X								
superiorparietal	3	70	* X				*									
superiorparietal	3	72	** X	*					*						*	
superiorparietal	3	73	* X													
superiortemporal	2	43	* X													
supramarginal	2	31	** X				*	**								
transversetemporal	8	10	** X					*								

Supplementary Video 1

This video shows the sequence of events in the task for boards of different size for one of the participants in the experiment. In each trial, participants click on two tiles. If they match, the tiles turn green, otherwise, the tiles turn black again. The goal is to find all matching pairs. See **Methods** for an expanded description of the task.