

1 Title: **Hippocampal place cells as a cryptographic tool that enables**
2 **animals to secretly cache and retrieve their food**

3

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11

12 **Abstract**

13 For animals, the ability to hide and retrieve valuable information, such as the location of
14 food, can mean the difference between life and death. Here, we propose that to achieve
15 this, their brain uses spatial cells similarly to how we utilize encryption for data security.
16 Some animals are able to cache hundreds of thousands of food items annually by each
17 individual and later retrieve most of what they themselves stashed. Rather than memorizing
18 their cache locations as previously suggested, we propose that they use a single
19 cryptographic-like mechanism during both caching and retrieval. The model we developed
20 is based on hippocampal spatial cells, which respond to an animal's positional attention,
21 such as when the animal enters a specific region (place-cells) or gazes at a particular
22 location (spatial-view-cells). We know that the region that activates each spatial cell remains
23 consistent across subsequent visits to the same area but not between areas. This
24 remapping, combined with the uniqueness of cognitive maps, produces a persistent crypto-
25 hash function for both food caching and retrieval. We also show that the model stores
26 temporal information that helps animals in food caching order preference as previously
27 observed. This behavior, which we refer to as crypto-taxis, might also explain consistent
28 differences in decision-making when animals are faced with a large number of alternatives
29 such as in foraging.

30

31

32 Main Text

33

34 Animals have much to hide. Some species evade potential predators or prey by finding cover
35 or by using camouflage (1), mimicry, and other means of disguise (2). Others conceal their
36 eggs or offspring, mask an illness or an injury to avoid being targeted by predators (3), or
37 stash valuable resources, such as food.

38

39 Scatter hoarding is probably the largest-scale manifestation of secretive behavior in the
40 animal kingdom. Many species of animals engage in this behavior, which involves storing
41 food at multiple cache sites to preserve it for times when food is scarce (4). Several bird
42 species, such as the Siberian tit (*Poecile cinctus*), were observed to cache over 500,000 items
43 per individual in one year (4). While much of the research on scatter hoarding was
44 conducted on birds, this behavior is not specific to them (4): squirrels (5), chipmunks (6),
45 and even foxes (7, 8) stash food for times of need. As caching sites cannot be defended, the
46 success of this strategy is often contingent on an animal's ability to keep the stashes away
47 from prying eyes and hard to find (5).

48

49 Once the valuables are stashed, scatter hoarders are faced with the considerable challenge
50 of retrieving the hidden items. It was shown that hoarding birds do not randomly seek out
51 cached food (9); rather, they mainly retrieve that which they had themselves hidden – a
52 remarkable feat, especially given the large number of cache sites (10). In the 1950s, Olof
53 Swanberg observed that almost 90% of Eurasian nutcracker (*Nucifraga caryocatactes*)
54 excavation holes contained cracked nutshells, indicating successful retrievals (4). In one
55 elegant experiment, Stevens and Krab attached tiny magnets to the legs of marsh tits
56 (*Poecile palustris*) (12). The birds were then offered serially numbered peanuts labeled with
57 a radioactive isotope, enabling the researchers to locate each bird's caching sites using a
58 scintillation counter (13). Magnet detectors were placed at each location to detect the
59 presence of marked birds. During the experiment, the birds retrieved about 25% of their
60 own stored food, while none of the control caches (set up by the researchers) were
61 activated. The actual retrieval rate was probably higher, but the experiment faced some
62 technical hurdles (4).

63

64 The ability to retrieve items from cache sites depends on spatial information such as visual
65 cues. In (14), black-capped chickadees (*Poecile atricapillus*) were placed in an enclosure and
66 their food-caching behavior was tracked. Object rearrangement around the enclosure
67 greatly impaired the chickadees' ability to find their cache sites; manipulation of prominent
68 global landmarks (large cardboard cutouts and a poster) had a much stronger effect on the

69 birds' retrieval performance than small proximal objects (5-cm squares). Shifting objects by
70 as little as 20 cm to the right significantly decreased the chickadees' ability to recover the
71 food. Moreover, in almost 70% of the cases, the birds searched within 5 cm of the location
72 implied by the more prominent landmarks, with a mean displacement of around 20 cm.
73 Assuming this is approximately the caching resolution, the finding indicates that a small
74 area of 10x10 meters can hold as much as 2,500 potential caching sites.

75

76 The hippocampus plays a central part in the remarkable cognitive feat of caching (9). This
77 is not surprising, as the hippocampus is known to be involved in processing spatial
78 information in the brain (11). A large subpopulation of neurons within the hippocampus in
79 animals such as mice, rats, and bats exhibit *place-cell* behavior; that is, they increase in their
80 spike rate in response to the animal's entering a specific region within a given site (usually,
81 but not always, one region per cell). The region activating each place cell often changes
82 when the animal moves to a new area, often in an unpredictable manner. However, if the
83 animal returns to a site previously visited, the place cell's receptive fields also return to their
84 previous arrangement, and this change happens practically instantaneously. This
85 remapping of the receptive field within a given environment is mostly insensitive to
86 landmark manipulations. In primates, we usually find a related type of cells referred to as
87 spatial view cells. These cells respond remotely when an animal is gazing at a specific region,
88 independently of the animal's location or head direction (12).

89

90 A well-known homolog to the mammalian hippocampus also exists in birds, with similar
91 involvement in spatial and episodic memory (13). Hippocampus size in birds was found to
92 correlate with birds' ability to stash food. Although the interpretation of this correlation is
93 under debate (14, 15), animals that used more cache sites generally had a larger
94 hippocampus than non-caching bird species (16, 17). In addition, even within the same
95 species, the size of the hippocampus was found to be larger in individuals dwelling in
96 harsher environments that makes them more dependent of the cached food (18). Moreover,
97 hippocampal neurogenesis has a seasonal element and seems to correlate with caching
98 activity throughout the year (19). For many years, the spatially responsive cells found in
99 avian brains were less related to a fixed position in space and more related to the challenge
100 the animal faced such as the position of a goal within a maze (20). Only very recently the
101 existence of place cells was demonstrated in the tufted titmouse (*Baeolophus bicolor*) (21).

102

103 Taken together with the fact that the hippocampus is involved in memory, these
104 observations have led researchers to hypothesize that caching requires some form of
105 spatial and episodic memory (22).

106

107 Yet as birds and other animals need an internal mechanism to guide them to stash food in
108 specific locations, the same mechanism can also be used to direct them to the exact same
109 locations while retrieving the food in that area. Such a mechanism may serve as a mnemonic
110 device (as suggested in (23)) or possibly replace the need for memory altogether. Such a
111 pseudo-random approach is much simpler than remembering hundreds of thousands of
112 stashing sites while still supporting all the existing empirical evidence. The guidance is
113 based on prominent landmarks in the terrain, such as trees and rocks, which are not likely
114 to substantially change over time, and can be used in the subsequent cache retrieval. And
115 we already know of a specific set of neurons to be able to do precisely this – the previously
116 mentioned hippocampal spatial cells. Spatial cells are unique to each individual, they assign
117 scores and rankings (using spike rates) to different locations within each area, they persist
118 over time, and remap when in the same area. We show how these properties allow animals
119 to find their cache sites efficiently and secretly.

120

121 ***Cryptography in the brain***

122 A mechanism, or mapping, that can facilitate efficient hiding and retrieval of multiple cache
123 sites without relying on memory would need to have several basic properties. From a
124 theoretical perspective, the class of methods that achieve this is known as cryptographic-
125 hashing functions (or crypto-hashes, for short), which, as the name suggests, are comprised
126 of two components: hashing functions and cryptographic keys (24).

127

128 In this context, hashing refers to a class of functions that map arbitrarily complex data
129 (images, texts, audio files, and others) to a fixed size lower-dimensional representation.
130 Computer applications often use crypto-hashes to store objects into memory efficiently by
131 mapping them directly to a memory location (a type of a mnemonic device). In the case of
132 food caching, hashing can be used to map a set of landmarks within and around an area
133 onto a selected caching site within that area (Figure 1A). Efficient hash functions are such
134 that the probability of assigning different cues the same output is kept to a minimum; This
135 property reduces the possibility of collisions and redundancies that can occur when two
136 different inputs result in the same output. It also makes better use of all the available
137 resources – in the case of animals allowing the use of the entire area for caching.

138

139 Unlike standard hash functions, crypto-hashes incorporate an additional entity – a private
140 key that renders the mapping unique to the key owner (24). Assuming no two individuals
141 have the same key, it also means that the mapping will result in unique caching sites within
142 the same area (Figure 1B). Another valuable property of crypto-hashes is that it is often

143 difficult to infer the key from a small number of examples, so even if another animal finds
144 several caches, it will not be able to deduce the location of all others.

145

146 A straightforward and biologically plausible realization of crypto-hashing is through a
147 simple two-layer neural network model with sparse connectivity (Figure 1C; see
148 supplementary information). The first layer, the input layer, represents the visual cues
149 (landmarks) within a given patch of land (Figure 2A, 2B). The second layer is a 2D lattice of
150 spatial neurons, in which each neuron points to a specific location in a given area (Figure
151 2C). The firing rate of each spatial neuron corresponds to the likelihood of choosing its
152 particular location as a caching site. The spatial neurons are sparsely innervated by the
153 input neurons.

154

155 In our model, we set the number of connections to a constant, typically equivalent to the
156 number of landmarks the model uses (usually four). This sparse connectivity helps maintain
157 a low number of potential cache sites by the output layer. A simple equation can summarize
158 the activity of each spatial neuron

159

$$C_{x_i, y_i} = \left| \sum_{x, y} w_{x, y}^i I_{x, y} \right|$$

160

161 where C_{x_i, y_i} is the score, or spike-rate, of the spatial neuron pointing to coordinate x_i, y_i of
162 the output grid; $I_{x, y}$ is the input from coordinates x, y ; and $w_{x, y}^i$ represents the strength of
163 the connectivity between $I_{x, y}$ and C_{x_i, y_i} . The strength, or weight $w_{x, y}^i$, of the connections was
164 assigned randomly at between one and minus-one. The inputs were also set in the range
165 one and minus-one, where the absolute magnitude represents the landmark's prominence
166 (one is very prominent and zero is designated as not noticeable). The sign represents the
167 landmark type, for example positive values represent "trees", and negatives represent
168 "rocks". The scores of the output neurons C_{x_i, y_i} effectively determine the probability of their
169 target area to be used as a cache site. We use the absolute value to keep the outputs
170 positive, although it has no computational benefit to the model. Nor is the choice to
171 distinguish between two types of objects by allowing negative inputs.

172

173 This neural network is a crypto-hash function, as it fulfills the three essential properties: (1)
174 It maps a complex terrain into a point with minimal overlapping probability across the
175 terrain or (2) across subjects (Figure 3A, 3B), and (3) reconstructing or decrypting the
176 mapping from examples is difficult. The third point stems from the fact that the connection
177 to each output-layer neuron is chosen randomly and independently of the others. Thus it is
178 effectively equivalent to holding a unique key for each neuron.

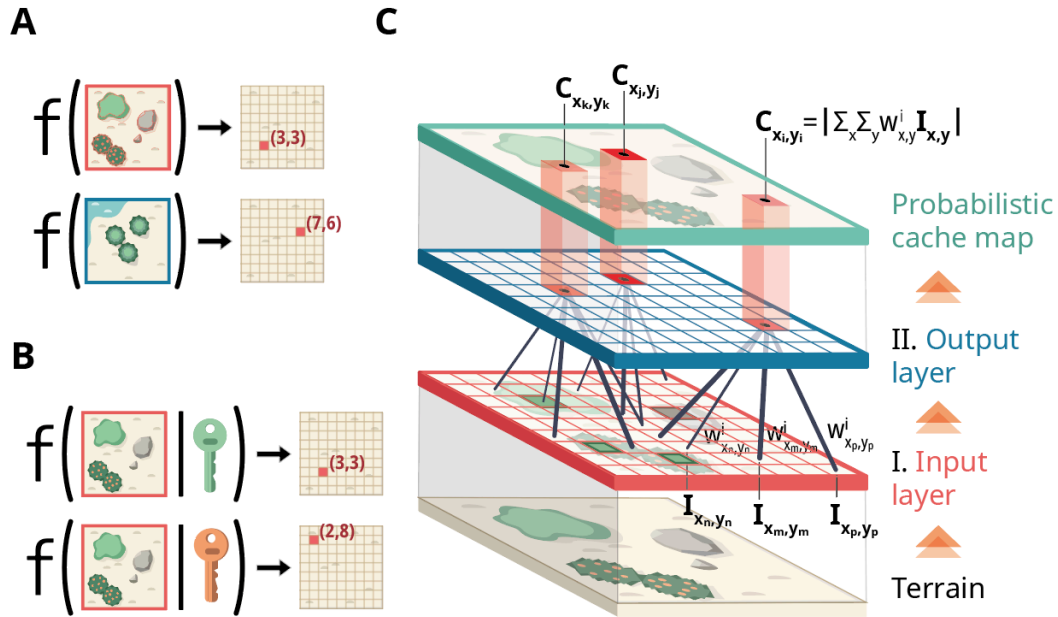


Figure 1. **Cryptographic mechanisms in the brain.** (A) Hash functions take high-dimensional objects (a map of a complex terrain, for example) and map them into a low-dimensional representation such as a point within that terrain. (B) Crypto-hash functions also include a private key that makes mapping the same object unique across individuals with different keys. (C) *Crypto-hashing in a two-layer neural network.* Each neuron $I_{x,y}$ in the input layer represents landmarks within a small square area. We assume two types of landmarks, which we refer to as ‘trees’ and ‘rocks’. Neurons that point to trees are assigned a positive value, rocks get negative values, and if no object is within the neuron’s receptive field, it is set to zero. The absolute value of $I_{x,y}$ corresponds to an object’s prominence; thus, prominent trees will get +1, smaller trees - 0.5, and small rocks may be assigned a value of - 0.3. The spatial output layer is a 2D mesh that assigns a caching score to each location within the site. The higher the score, the more likely this location would be used for caching. Each neuron in the output layer is innervated by a small number of input neurons. In all of our simulations, we matched this number to the number of landmarks the model uses.

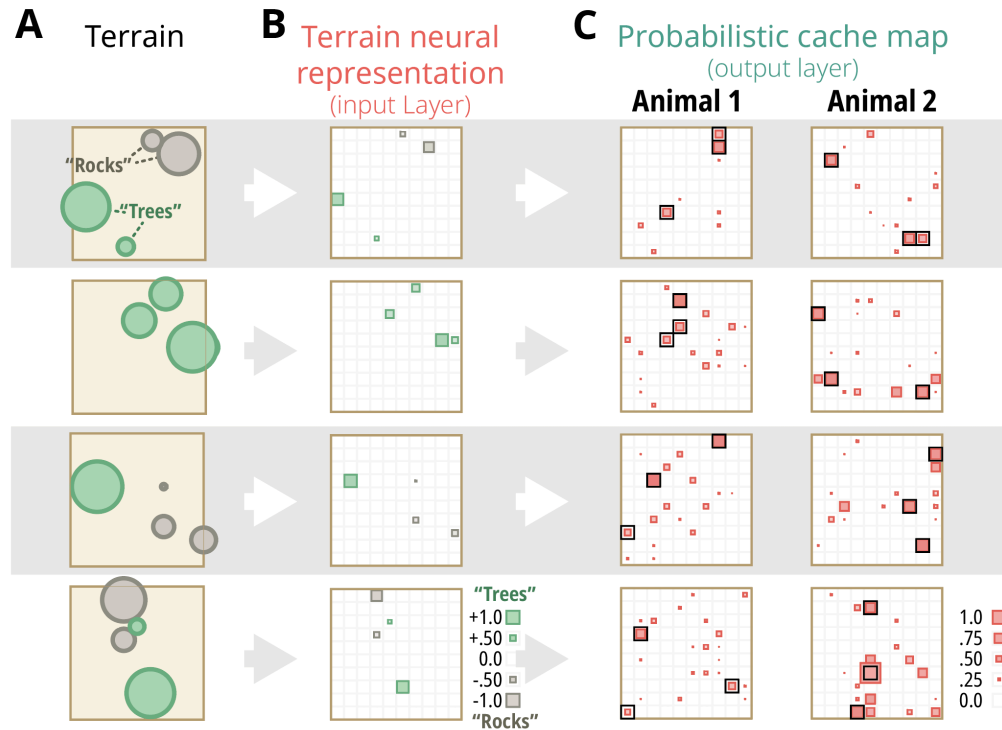


Figure 2. **Using spatial features to map cache sites without requiring brain plasticity.** (A-C) Four examples of the outcome of a crypto-hash neuronal network (in rows). (A) We simulated a terrain with four prominent landmarks by randomly choosing four cells within a 10x10 grid. The cells were assigned random values between -1 and +1, so that the absolute value represents the prominence of the spatial feature (cells with values close to +1 and -1 being the most prominent), and the sign represents the type of object. We refer to positive-valued cells as “trees” and negative cells as “rocks” for brevity. (B) The representation of the landscapes from (A) in the neural network’s input layer. The size of the colored inlaid boxes represents the object’s prominence and their color its sign (green for positive values or “trees”, and gray for negatives or “rocks”). (C) The output of the target layer of two randomly chosen neural networks (Animal 1 and 2) in response to the inputs in (B). The output layer creates a unique probabilistic map of possible cache sites.

179

180 The result can serve as a traditional crypto-hash function by choosing the target neuron
181 with the highest score as the mapping outcome (see Materials and Methods). However, a
182 probabilistic map with multiple outcomes of varying probabilities – apart from being more
183 biologically feasible – also provides several benefits. The most straightforward benefit is
184 that it allows for an arbitrary number of caching sites within each area by choosing the
185 spatial neurons with the top scores.

186

187 Another valuable property of probabilistic maps is that they allow the addition of temporal
188 considerations into caching behavior (22). Assuming the order of food recovery starts with

189 locations that have higher scores, items with higher nutritional values or perishable items
 190 (such as dead insects, as opposed to seeds) could be stashed in places with higher scores –
 191 making them more likely to be recovered prior to items assigned to lower-scored locations
 192 (Figure 3C). In addition, avoiding previously excavated sites requires only memorizing the
 193 score of the last excavated and choosing only sites with a lower score (we refer to this
 194 behavior as bookmarking).

195
 196 Finally, we did not address how mappings in the model are kept allocentric and invariant to
 197 the animal's position. A straightforward approach to achieve such invariance was
 198 suggested in an elegant paper about geometric hashing (25). The method there is based on
 199 choosing two prominent objects in the area and using them to scale and align all landmarks.
 200 The vector connecting the two most prominent landmarks defines the direction axis and
 201 the distance between them sets the scale unit. Using this approach, we can obtain a model
 202 that is insensitive to affine transformations.

203

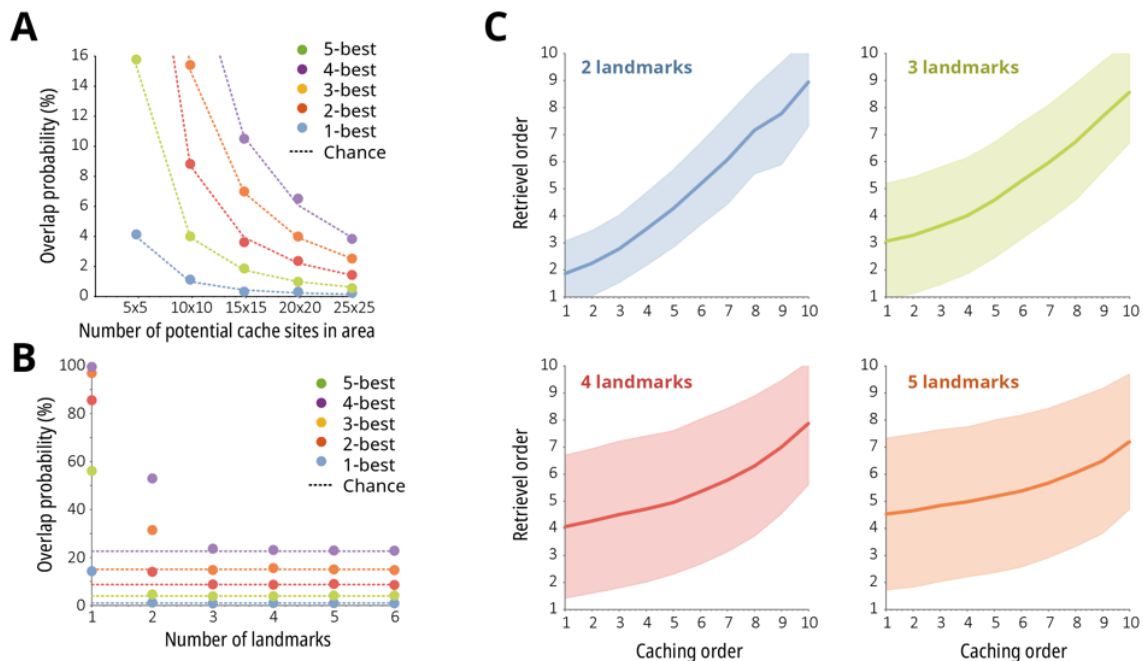


Figure 3. **Properties of a crypto-hash neural network.** The probability of overlapping sites between two random networks as a function of (A) potential cache sites and (B) the number of landmarks the network uses. The different colors correspond to the number of caches used in each area. The dotted lines are the overlap as expected from a random choice of sites. (C) *The probabilistic nature of the target layer scores allows the network to maintain temporal dynamics.* We assume that caching and retrieval order are determined by the target-layer score, from highest to lowest. If the choice is not absolute but probabilistic, we still get the same temporal dynamic in both phases. The shaded area around each line represents the standard deviation.

204

205 **METHODS**

206 **Landmarks and terrain**

207 While the algorithm is not sensitive to the number of landmarks, for the sake of simplicity,
208 we assumed a fixed number of landmarks within each area - four, in this paper. These
209 landmarks were divided into two categories, which we refer to as “trees” and “rocks”. The
210 locations of the landmarks were chosen randomly and uniformly from an n-by-n square grid
211 (in most cases we use n=10). Each landmark was then assigned a random value between
212 minus one and one that signifies the objects category and prominence: Cells that have
213 positive values are referred to as trees (values between zero and one), while rocks had
214 negative numbers (between zero and minus one). The absolute value of each landmark
215 signifies its prominence - so prominent trees have values closer to one and prominent rocks
216 have values closer to minus one. Zero marks a no-object. The outcome is a sparse n-by-n
217 matrix $S_{n \times n}$ with values that vary between minus one and one.

218

219 **Crypto-Hash Functions**

220 Hash functions map data with arbitrary dimensions to a fixed-length value (24). In
221 mathematical terms, a hash function $g_p(\bar{s})$ is such that

222

223

$$g_p(\bar{s}) = \bar{y}_p$$

224

225 where $\bar{s} \in S$ is a vector of arbitrary length, and $\bar{y}_p = (y_1, y_2, \dots, y_p) \in \mathcal{Y}_p$ is a vector of a fixed-
226 length p . Since the length of \bar{s} is often larger than that of \bar{y}_p hash-functions can be viewed
227 as a special case of dimensionality-reduction.

228

229 An optimal hash function is such that the probability of mapping two inputs onto the same
230 output is minimal, or, equivalently, that all outputs values should have (roughly) the same
231 probability. This principal of uniformity can be formulated as

232

$$p(g_p(\bar{s}) = y) \approx \frac{1}{|\mathcal{Y}_p|}$$

233

234 where $|\mathcal{Y}_p|$ is the cardinality (number of elements or size) of the set \mathcal{Y}_p of all possible output
235 values. Because of their uniformity, hash functions are often used in data storage and
236 retrieval tasks as they allow data access at nearly a constant time while requiring a storage
237 size that is only slightly larger than the space needed to store the data itself.

237

238 Crypto-hash functions introduce an additional term, a private-key k , to the basic hash
239 function

240

241
$$g_p(\bar{s}; k) = \bar{y}_p.$$

242

243 The key ensures that the mapping is unique, i.e. the probability that the same inputs
244 produce the same outputs for different keys is close to chance. Crypto-hash functions, like
245 hash functions in general, are deterministic, meaning that the same combination of input
246 and key will always produce the same output value. However, crypto-hash mappings are
247 also one-way-functions, meaning that they are difficult to invert; knowing an output value
248 gives very little information about the input or key.

249

250 **Crypto-Hash Neural Network**

251 Choice and retrieval of cache sites is based on prominent landmarks within a terrain.
252 Assuming $S_{n \times n}$ is the representation of the current area's terrain (see the 'simulated terrain'
253 section), our crypto-hash function can be defined as

254

(1)
$$g_p(S_{n \times n}; k) = (x, y)$$

255

256 where (x, y) is the cache coordinate within the area so that $x, y \in \{1, \dots, n\}$, and k is the crypto-
257 key.

258

259 A straightforward and biologically plausible to achieve this is using a neural network. We
260 define a two-layer network where, for simplicity, the neurons on both layers are organized
261 as a grid with x, y indices. The value of each neuron in the first layer $I_{x,y}$, which is the input
262 layer, is set according to the corresponding area tile or the (x, y) 'th cell in $S_{n \times n}$. Each output
263 layer neuron C_{x_i, y_i} was sparsely connected to the input layer, and the weights $w_{x,y}^i$ were
264 randomly distributed between minus-one and one. The value of output neurons is the
265 absolute value of the weighted sum of their inputs

(2)
$$C_{x_i, y_i} = \left| \sum_{x,y} w_{x,y}^i I_{x,y} \right|.$$

266

267 In order to get a crypto-hash function in the form (1) we can take the index of the maximal
268 value or

269

$$g_p(S_{n \times n}; k) = \underset{x', y'}{\operatorname{argmax}} C_{x', y'}.$$

270 In our case, a unique key k is obtained from the random choice of weights between the
271 neural network's layers.

272

273 However, as we mentioned in the text, keeping the function as a probabilistic mapping like
274 in (2) has several benefits and this is the form we use in the paper.

275

276 **DISCUSSION**

277

278 Although spatial cells, such as place cells have been extensively studied, the mechanism we
279 presented is one of the few explanations to how the brain might utilize these cells. We
280 proposed here that spatial cells can serve as the brain's crypto-hash functions, enabling
281 animals to hide food in unique cache sites and later to retrieve it. So far, there has been no
282 theory that explains what principles guide animals when choosing cache sites; If it was
283 merely a question of optimality, all animals might end up choosing the same sites, which
284 would lead to theft (or kleptoparasitism).

285

286 For brevity, we did not address how mappings in the model are kept allocentric and
287 invariant to the animal's position. A straightforward approach to achieve such invariance
288 was suggested in an elegant paper about geometric hashing (30). The method there is
289 based on choosing the two most prominent objects in the area and using them to scale and
290 align all landmarks. The vector connecting the two most prominent landmarks defines the
291 direction axis and the distance between them sets the scale unit. Using this approach, we
292 obtain a model that is insensitive to affine transformations (see supplementary
293 information).

294

295 While our focus here is on scattered hoarding, a similar mechanism may also be involved in
296 processes of decision making when the number of possibilities is large. A bee foraging for
297 nectar and pollen, for example, would benefit from choosing flowers less likely to have been
298 visited by other bees. The same function-driven mechanism (rather than memory-driven)
299 may also help steer migratory animals back to previously used nesting areas. And since the
300 hippocampus is involved in abstract knowledge in addition to spatial information (11), the
301 scope of decision-making might be much broader; Since diversity is a key characteristic of
302 all living system, it is tempting to think that humans' individualistic tendencies might also
303 be somehow related to our proposed brain circuitry.

304

305 While the work we presented is theoretical, it raises some obvious predictions. First, that
306 knowing the spiking patterns of spatial cells will enable us to determine cache site locations.
307 Moreover, if we know the remapping between sites well, we can use it to decrypt the internal
308 circuitry and predict cache sites in a new site that the animal is yet to visit. Finally, we predict

309 that the location of cache sites within a given area would be consistent across multiple hide
310 and retrieval iterations.

311

312 The instinct to choose cache sites that are both unique and obscure has a clear evolutionary
313 advantage. We therefore fondly suggest addressing this movement pattern as *cryptotaxis*
314 and the neurons involved as *crypto-cells*.

315

316

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329

330 **Competing interests**

331 Authors have no competing interests

332 **Data and materials availability**

333 All code is available online

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