1   Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the

2   question

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21 Abstract

22 Cognitive flexibility allows animals to readily acquire new information even when learning

23 contingencies may rapidly change, as is the case in highly variable, but predictable

24 environments. While cognitive flexibility is broadly thought to be beneficial, animals

25 exhibit inter- and intra-specific variation, with higher levels of flexibility associated with

26 reduced memory retention and vice versa. In this review, we discuss when and why such

27 variation may exist and focus specifically on memory and memory flexibility. We argue

28 that retained memories may negatively affect the acquisition of new information, most

29 likely via proactive interference, and available data suggest that there may be a trade-off

30 between memory retention and acquiring new memories. We discuss neurogenesis-

31 mediated forgetting as the mechanism reducing memory interference, as new neurons

32 enhance learning new information, but also cause forgetting of older memories. Selection

33 may be expected to favor either end of the continuum between memory retention and

34 memory flexibility depending on life history and environment. More stable environments

35 may favor memory retention over flexibility whereas rapidly changing environments may

36 favor flexibility over retention. Higher memory capacity also seems to be associated with

37 higher memory interference, so higher neurogenesis rates associated with forgetting of

38 unnecessary information may be favored when higher capacity is beneficial such as in

39 food-caching species. More research is necessary to understand if inter- and intra-specific

40 differences in the association between memory retention and flexibility are related to some

41 general ecological patterns, whether this association is heritable, and whether

42 developmental conditions and experience have different effects on this association in

43 different species.

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Introduction

49   Animals are able to modify their behavior due in part to their ability to learn new

50   information associated with relevant contingencies in their environment. However, relevant

51   contingencies often change and animals must be able to switch their behavioral responses

52   to fit new contingencies and this is usually referred to as cognitive flexibility. Behavioral or

53   cognitive flexibility has been defined by psychologists as the ability to reverse

54   contingencies while learning new information (Badre & Wagner, 2006). More flexible

55   animals can readily learn continuously changing contingencies. Traditionally, within a

56   laboratory context, an animal is thought to be cognitively flexible if it can successfully

57   learn new information while either keeping or forgetting older information. To test

58   cognitive flexibility, the "reversal-learning task" is often used. This task uses an

59   experimental paradigm where contingencies of previously learned associations are changed

60   or reversed (Anderson & Neely, 1996; Strang & Sherry, 2014). For example, in a color

61   association reversal-learning task an animal may be presented with two different color

62   handles, and is first trained that pressing the blue handle will result in reinforcement, while

63   pressing the green handle results in no reinforcement. After the animal has reached a set

64   performance criterion, the relationship is reversed, such that pressing the green handle now

65   results in reinforcement and pressing the blue handle results in no reinforcement. An animal

66   that scores highly on a cognitive flexibility task is one that takes fewer trials to extinguish

67   the previously reinforced behavior and only responds to the new contingency. Similarly, in

68   spatial reversal-learning task, changing the location associated with reward also allows

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69   testing for cognitive flexibility. In this case, a flexible individual is expected to learn the

70   new locations and stop visiting the location that no longer provides reward (e.g. Croston et

71   al. 2017). A standard serial reversal task frequently involves just a binary choice that keeps

72   changing between the same two available options with each reversal (two colors or two

73   spatial locations). An alternative version involves non-repeatable choices at each reversal

74   (e.g. different color at each reversal or different spatial location at each reversal).

75   Behavioral ecologists have greatly expanded the use of the term 'behavioral

76   flexibility' to include any behaviors that allow animals to adjust to changing environments,

77   including behavioral innovations and problem solving. Such diversification of the term has

78   produced confusion as different behaviors used to describe behavioral flexibility often have

79   different underlying neural and physiological mechanisms. This confusion prompted Audet

80   and Lefebvre (2017) to suggest that we should stop using the term flexibility and instead

81   focus on specific behaviors associated with flexibility.

82   Traditionally, cognitive flexibility has been viewed as a highly adaptive ability

83   (Dukas, 2004; Lefebvre, Reader, & Sol, 2004) that increases survival and reproductive

84   success (Snell-Rood, 2013). However, available data shows both inter- and intra-species

85   variation, with higher levels of flexibility associated with reduced memory retention and

86   vice versa. Throughout this review, we will consider (1) potential trade-offs among

87   memory retention, memory capacity, memory load, and cognitive flexibility, (2) forgetting

88   as a mechanism allowing this trade-off, (3) adult neurogenesis as a mechanism of

89   forgetting, and (4) future directions to investigate the proposed trade-offs. We will

90   specifically focus on memory and memory flexibility, which we define as the ability to

91   successfully learn new information when learning contingencies keep changing.

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4

93   *Why are some animals less flexible?*

94   One of the major questions in understanding the evolution of cognitive flexibility is why

95   there is inter- or intra-specific variation in cognitive flexibility and what are the

96   mechanisms underlying such variation. One of the earliest studies on this subject reported

97   that pigeons (*Columba livia*) were better at learning a reversal task (e.g. more flexible) but

98   showed worse memory retention, while goldfish (*Carassius auratus*) performed worse on

99   the reversal task (e.g. less flexible) but showed better memory retention (Gonzalez,

100   Behrend, & Bitterman, 1967). This study suggested that (a) species differ in memory

101   flexibility and (b) there appears to be a trade-off between cognitive flexibility and memory

102   retention.

103   Inter-specific variation in cognitive flexibility suggests that there should be a cost to

104   being cognitively flexible. Some of these costs may be energy-related, such that the energy

105   needed to maintain a long-term memory (Plaçais & Preat, 2013) or to process information

106   (Dukas, 1999; Mery & Kawecki, 2003). The physiological costs of cognition can affect

107   other traits like reproduction. For example, fruit fly (*Drosophila melanogaster*) lines

108   selected for enhanced learning abilities also showed a decline in larval competitive ability

109   (Mery & Kawecki, 2003).

110   Other costs might be related to potential trade-offs associated with cognitive

111   flexibility. While there is a paucity of comparative studies including both aspects of

112   cognitive flexibility (e.g. memory retention and memory flexibility), the few that do exist

113   are consistent with the idea of a trade-off between flexibility and memory retention and

114   suggest that a better ability in one is associated with a worse ability in the other.

115   Research on food-caching species exemplifies this trade-off. Food-caching black-

116   capped chickadees (*Poecile atricapillus*) with the overall better spatial memory ability than

117   non-caching dark-eyed juncos (*Junco hyemalis*), were less capable at learning a new

118   contingency after reversal, suggesting that older memories interfered with acquiring new

119   memories (Hampton, Shettleworth, & Westwood, 1998). Clark's nutcrackers (*Nucifraga*

120   *columbiana*), which are known for their extremely long lasting spatial memory, performed

121   significantly worse on a spatial reversal-learning task compared to their performance on an

122   initial spatial learning task (Lewis & Kamil, 2006). Finally, mountain chickadees (*Poecile*

123   *gambeli*) inhabiting high elevations performed worse on a spatial reversal-learning task

124   compared to low elevation chickadees (Croston et al., 2017; Tello-Ramos et al. 2018). At

125   the same time, our previous studies documented that high elevation chickadees performed

126   significantly better on an initial spatial memory task (both acquisition and retention), had a

127   larger hippocampus with more neurons, and exhibited higher rates of adult hippocampal

128   neurogenesis (Freas, LaDage, Roth, & Pravosudov, 2012). All of these findings are also

129   consistent with the idea of a potential trade-off between the ability to retain older memories

130   and the ability to rapidly acquire new memories.

131

132   ***Memory interference resulting in a major trade-off***

133   The cost of learning new information reflects the fact that the brain and the neural networks

134   that store memory patterns are finite, with networks eventually reaching saturation (i.e.,

135   memory load or capacity). Because memory storage or capacity is limited, the acquisition

136   of new memories may interfere with old memories, and vice versa, specifically when new

137   and old memories are similar (Anderson & Neely, 1996; Wixted, 2004). The essential

138   problem associated with interference is that the retrieval cues available at the time of recall

139   fail to access the target memory (Anderson & Neely, 1996). One way to explain this

140   phenomenon is that when a cue is linked to more than one memory, different memories

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141   compete for access during the recall processes (Bjork, 1989). Interference should increase

142   with the number of competitors or distractors associated with the same cues. In humans, for

143   example, memory recall performance decreases when the number of memories that are

144   paired with the same cue increases - the cue-overload principle (Watkins & Watkins, 1976).

145   On the other hand, when cues and contexts used to learn are more dissimilar, interference

146   should decrease. For example, in Clark's nutcrackers, memory performance improved in a

147   spatial reversal learning task when given new spatial cues during the reversal phase

148   compared to performance in a reversal task with the same spatial cues as during the initial

149   learning (Lewis, Kamil, & Webbink, 2013). Similarly, lab rats showed significant

150   interference after learning a second task but such interference was significantly reduced

151   when the context, such as light, size of arena, and texture of arena, of each task was made

152   increasingly different from each other (Rodriguez, Borbely, & Garcia, 1993). Interference

153   is thought to occur specifically during memory retrieval (or recall) and depending on

154   whether old memories or the formation of new ones is impaired, interference can be

155   classified as retroactive or proactive interference.

156   Retroactive interference occurs when previously learned information is affected, or

157   forgotten, by learning new, similar information. For example, honeybees (*Apis mellifera*)

158   that were trained to turn right on a green land mark first and then trained to turn left on a

159   blue landmark, decreased their performance on a later test for the first task (Cheng &

160   Wignall, 2006).

161   Proactive interference occurs when previously learned information interferes with

162   learning and remembering new information. Proactive interference appears to be one of the

163   main mechanisms affecting cognitive flexibility because it may directly influence learning

164   of new information. Most common tests for proactive interference include learning

165   reversals and serial learning reversal tasks. When serial reversal task is used with just two

166   possible choices (e.g. Cauchloix, Hermer, Chaine, Morand-Ferron, 2017), animals are

167   expected to learn the rule that they need to switch when the previously rewarding choice is

168   no longer rewarding. Such task does not allow testing for memory retention and how

169   memory retention may affect learning of new associations via proactive interference. A

170   more appropriate reversal task (whether single or serial reversal) should require an animal

171   to learn new associations that have not been used before during each reversal stage. Such

172   approach allows direct assessment of both retention of memories of previously rewarded

173   associations and acquisition rates of new associations.

174   For instance, highly specialized food-caching Clark's nutcrackers that were given

175   either one or two "lists" of rewarded locations performed worse during recall of the second

176   list than during the recall for the first list, demonstrating proactive interference (Lewis &

177   Kamil, 2006). Likewise, Florida scrub-jays (*Aphelocoma coerulescens)* that performed

178   better in an initial learning task did worse in a reversal task and vice versa, again suggesting

179   there may be a trade-off between initial and reversal learning ability (Bebus, Samll, Jones,

180   Elderbrock, & Schoech, 2016). If learning a useful association in the environment interferes

181   with learning a new association in the future, animals would not be able to quickly adjust

182   their behavior in a rapidly changing environment.

183   Based on human studies, it appears that retroactive interference is stronger when the

184   delay between learning new information and recalling old information is short. When more

185   time has passed between learning new information and recalling the older information,

186   retroactive interference decreases. Conversely, proactive interference increases with more

187   time between learning new information and recalling it – older information is recalled more

188   accurately than the newer information as more time has passed (Postman, Stark, & Fraser,

189   1968; Storm & Bjork, 2016).

190   Overall, it appears that the extent of proactive interference is a critical mechanism

191   involved in the trade-off between memory retention and the ability to acquire new

192   memories. Better memory retention seems to be associated with a higher level of proactive

193   interference and hence with less cognitive flexibility while higher cognitive flexibility

194   appears to be associated with less proactive interference and with worse memory retention.

195   As such, the rest of this review will focus on proactive interference.

196

197   *Forgetting as a mechanism reducing interference and increasing cognitive flexibility*

198   At least one mechanism known to reduce proactive interference is forgetting, as forgetting

199   allows the acquisition of new memories without interference with older memories

200   (Anderson & Neely, 1996). Forgetting, described as the absence of expression for

201   memories that once caused expression, is no longer regarded as memory failure (Kuhl &

202   Wagner, 2009). Instead, given the dynamic nature of the environment, forgetting is likely

203   an essential component of any adaptive memory system that increases behavioral and

204   cognitive flexibility and therefore, remembering and forgetting are intimately related (e.g.

205   Kraemer & Golding 1997). Although forgetting might reflect actual memory loss (decay), it

206   can also be explained as a failure to retrieve existing memories (interference) and can

207   reduce memory load. In humans, deliberate attempts to forget specific information can

208   improve learning new information (Festini & Reuter-Lorenz, 2014). Imagine for example

209   the memory task of a restaurant cook, for whom it would be advantageous to forget an

210   order once it has been completed. The advantage of forgetting a completed order, is that it

211 reduces confusion (proactive interference) when trying to remember other current orders

212 (Bjork, 1970). Work on animals implicated adult neurogenesis as one of the main neural

213 mechanisms that facilitate forgetting (Frankland, Köhler, & Josselyn, 2013).

214

215 *Neurogenesis as a mechanism of forgetting and reducing proactive interference*

216 Adult neurogenesis is a process of neuronal replacement during adulthood first described

217 by Altman and Das in the 1960´s (Altman & Das, 1965,1967). Adult neurogenesis consists

218 of neuron proliferation, migration, survival, and finally incorporation into the existing

219 neural circuits, usually in the hippocampus, a brain region involved in memory (van Praag,

220 Christie, Sejnowski, & Gage, 1999). Adult hippocampal neurogenesis does not result in

221 increasing the total number of neurons – instead adult neurogenesis and apoptosis, or

222 neuron death, operate simultaneously and result in adult neuron replacement (Barnea &

223 Pravosudov, 2011; Olson, Eadoe, Ernst, & Christie, 2006; van Praag et al., 1999). The

224 majority of new neurons actually die without being recruited into neural circuits, and it is

225 hypothesized that new neurons may form a neurogenic reserve that can provide new

226 neurons when needed (Kempermann, 2008).

227   Most research on adult neurogenesis has been focused on its role in facilitating new

228 learning and almost all existing hypotheses about the function of neurogenesis suggest that

229 it improves learning (Gould et al. 1999; van Praag et al., 1999; Kempermann 2008).

230 Ecological research, in particular, primarily considers neurogenesis as the neural

231 mechanism that enhances learning of new information (Barnea & Pravosudov, 2011).

232   More recently, however, it was discovered that adult neurogenesis is also directly

233 involved in forgetting and that enhanced learning of new information associated with

234 neurogenesis appears to be, at least in part, due to forgetting of older information (Akers et

235 al., 2014; Epp et al. 2016). New findings show that new neurons enhance the acquisition of

236 new memories, but at the same time death of old neurons associated with incorporation of

237 new neurons appears to cause forgetting of older memories which decreases proactive

238 interference (Akers et al., 2014; Epp et al. 2016). Interestingly, it seems that apoptosis of

239 old neurons is not random, but rather a targeted replacement of old memories that are no

240 longer useful with new neurons produced by neurogenesis.

241   Learning and memory, and the decrease in proactive interference are positively

242 associated with adult neurogenesis rates because at least one function of neurogenesis

243 represents a decay process that continually clears out old memories from the hippocampus

244 (Frankland et al., 2013). Newly born cells are different compared to older neurons; they are

245 both more excitable and more sparse, which is why adult neurogenesis seems to promote

246 pattern separation, a process by which overlapping patterns of neural activation are mapped

247 to less overlapping representations, effectively reducing interference (Becker, 2005).

248 Computational models of neural networks also show that neuronal turnover should improve

249 learning of new information specifically by discarding older memories (e.g. forgetting)

250 (Chambers, Potenza, Hoffman, & Miranker, 2004; Crick & Miranker, 2006; Weisz &

251 Argibay, 2012).

252   It appears that hippocampal neurogenesis directly mediates the continuous process

253 of forgetting older hippocampus-dependent memories by reconfiguring neural circuits and

254 resulting in the dissociation of memory cues with previously stored memories (Akers et al.,

255 2014). Neurogenesis is more active in younger animals, which are also more forgetful (and

256 more flexible), but experimentally reduced hippocampal neurogenesis rates in adulthood

257 result in longer lasting memories (but less flexibility; Akers et al., 2014). For instance, in

258   adult mice, experimentally increasing neurogenesis rates induced forgetting, while in young

259   animals with naturally occurring higher neurogenesis rates, experimental reduction in

260   neurogenesis increased memory retention (Akers et al., 2014; Kitamura et al., 2009). In a

261   different study, increased neurogenesis rates associated with more running resulted in

262   reduced memory retention, but also resulted in better performance in a reversal learning

263   task (Epp et al. 2016). Experimental suppression of adult neurogenesis resulted in better

264   memory retention but also in worse performance in a reversal learning task (Epp et al.

265   2016). These findings support the idea that increased neurogenesis reduces proactive

266   interference and enhance learning of new information, but at a cost of reduction in memory

267   retention (e.g. forgetting), while reduced neurogenesis enhances memory retention but

268   impedes learning new information because of proactive intereference.

269   As mentioned earlier, the neurogenic reserve hypothesis (Kempermann, 2008)

270   suggests that new neurons form a pool that may be used when needed. This hypothesis is

271   consistent with the idea of adult neurogenesis aiding forgetting and not just the idea that

272   new neurons are recruited only to increase memory ability (e.g. Johnson et al., 2010).

273   Incorporation of new neurons into the existing circuits should disrupt older memories (e.g.

274   forgetting), therefore, at the time when animals may consistently acquire new memories,

275   such as the case with food-caching animals when they actively store food, they would not

276   benefit from higher neurogenesis as it will result in forgetting existing caches as memories

277   of new caches are being constantly formed.

278   Overall, there is mounting evidence that adult hippocampal neurogenesis improves

279   the acquisition of new information while at the same time causing forgetting and increasing

280   cognitive flexibility (Akers et al. 2014; Swan et al. 2014; Garthe, Behr, & Kempermann,

281   2009; Burghardt et al. 2012; Frankland et al. 2013; Weisz & Argibay 2012; Hardt, Nader,

282   & Nadel, 2013; Kitamura et al. 2009; Guskjolen, Epp, & Frankland, 2017; Feng et al. 2001;

283   Martinez-Canabal 2015; Becker, MacQueen, & Wojtowicz, 2009; Epp, Mera,

284   Kohler,Jesselyn & Frankland, 2016; Yau, Li, & So, 2015).

285

286   ***Need to re-evaluate how we view neurogenesis in many ecologically relevant paradigms***

287   Most of research on forgetting and neurogenesis have been conducted with model systems

288   such as lab rodents and focused directly on the mechanistic relationship between

289   neurogenesis, memory and forgetting. At the same time, there is great historical paucity of

290   research addressing inter- and intra-specific variation in this relationship and how such

291   variation might be associated with different selection pressures despite great interest in

292   inter- and intra-specific variation in adult neurogenesis rates (Barnea & Pravosudov 2011).

293

294   *Food-caching animals*

295   Recent advances in our understanding of adult neurogenesis involvement in forgetting

296   requires reconsideration of most current ecologically-based hypotheses about role of adult

297   neurogenesis. Previously, adult hippocampal neurogenesis has always been considered only

298   as a mechanism enhancing spatial learning (Barnea & Pravosudov, 2011). Starting with

299   Barnea and Nottebohm's (1994) study reporting seasonal differences in hippocampal

300   neurogenesis and connecting these differences to variation in food caching activity, all

301   studies of neurogenesis in food-caching birds and mammals attempted to explain any

302   differences in hippocampal neurogenesis rates by memory benefits associated with

303   increased neurogenesis rates (Barnea & Nottebohm, 1994; Hoshooley & Sherry, 2007;

304   Roth et al., 2012; LaDage et al., 2010, 2011; Barker et al., 2005; Johnson et al., 2010).

305   While species/population comparisons did find that animals with higher demands for food

306 caches indeed have higher hippocampal neurogenesis rates (Roth et al., 2012; Freas et al.,

307 2012), these results might also be explained by both improvements in memory flexibility

308 allowing learning new information and forgetting associated with retrieval of more food

309 caches.

310   A lack of any significant associations between adult hippocampal neurogenesis rates

311 and food-caching activity in all previous seasonal comparisons (review in Pravosudov &

312 Roth 2013; Pravosudov et al., 2015) is inconsistent with the previous hypotheses. If

313 hippocampal neurogenesis is involved specifically in memory improvements associated

314 with more food caching, it is expected that within a year, higher food caching activity

315 should be associated with higher neurogenesis rates (e.g. Barnea & Nottebohm, 1994).

316 None of the available data match these predictions (Hoosholey & Sherry, 2004; Hoshooley

317 et al., 2007; Hoosholey & Sherry, 2007). Even the first landmark study (Barnea &

318 Nottebohm, 1994), which is always used as an example of association between adult

319 hippocampal neurogenesis and food caching, actually showed highest neuron incorporation

320 rates by end of November-December in birds injected with a new neuron marker in October

321 (Pravosudov et al., 2015). The peak of food caching, on the other hand, is usually in

322 September-early October (e.g. Pravosudov, 2006), so these new neurons were not likely

323 there during the peak of food caching.

324   The observed seasonal patterns, however, fit much better if we assume that higher

325 neurogenesis rates are associated with cache retrieval-based forgetting. Chickadees start

326 retrieving caches in late fall and likely continue through spring (e.g. Pravosudov, 2006). At

327 the same time, the actual cache retrieval pattern may depend on weather, availability of

328 other food, etc. – and so variation in highest neurogenesis rates between November and

329 spring may be explained by variation in cache retrieval activity.

330   In the lab, chickadees that were allowed to cache and retrieve food on a daily basis

331   had higher hippocampal neurogenesis rates than birds experimentally prevented from

332   caching (LaDage et al., 2010). Again, this finding is consistent with neurogenesis-based

333   forgetting as chickadees were both caching and retrieving caches. Interestingly, in non-

334   caching, parasitic cowbirds (*Molothrus ater*), which use spatial memory for host nests

335   throughout the breeding season, the highest neurogenesis was reported in late summer after

336   breeding (Guigueno et al. 2016), which is also consistent with the idea of neurogenesis-

337   based forgetting of no longer relevant information.

338

339   *Migratory behavior*

340   It has been hypothesized that migratory behavior is associated with more spatial memory

341   use and at least some comparisons indeed showed that compared to non-migratory

342   subspecies, migratory subspecies performed better in a spatial memory task (Cristol et al.,

343   2003; Pravosudov et al., 2006). Migratory birds were hypothesized to have higher reliance

344   on spatial memory similar to food-caching birds since they may need to remember details

345   of permanent stopover locations as well as details of both breeding and wintering areas.

346   Migratory species/subspecies have larger hippocampus than non-migratory species, but at

347   least in one comparison of migratory and non-migratory white-crowned sparrows

348   (*Zonotrichia leucophrys*), adult migratory birds had higher hippocampal neurogenesis rates

349   than adult non-migratory sparrows, but similar to that in juveniles from both subspecies

350   (LaDage et al., 2011). Non-migratory adults, on the other hand, had lower hippocampal

351   neurogenesis rates than the juveniles from both subspecies. Reduction in hippocampal

352   neurogenesis rates with age is a well-known phenomenon and it has also been associated

353   with more cognitive flexibility and less memory retention in younger individuals and the

354 opposite relationship in older animals (Akers et al. 2014). Migratory adults, however, did

355 not have reduced neurogenesis rates compared to juveniles, at least at the time of sampling

356 during fall after they arrived at the wintering grounds. Higher neurogenesis at that time

357 might be associated with discarding past memories formed during migration allowing for

358 higher memory flexibility at wintering grounds. Since no comparative data are available on

359 either memory retention or memory flexibility in migratory and non-migratory

360 species/subspecies, it is too early to make any conclusions about potential trade-offs among

361 memory retention, memory capacity/load, memory flexibility and adult neurogenesis. But

362 we can make predictions based on hypothesized associations that migratory species (1)

363 should have higher memory capacity and larger memory load and (2) should be less

364 cognitively flexible compared to non-migratory species. Higher neurogenesis rates in

365 migratory birds may be associated with the need to reduce memory load and to reduce

366 proactive interference. In this case, similar to that in food-caching species, neurogenesis

367 might function to reduce the negative effects of proactive interference associated with

368 stronger memories.

369

370 **Memory capacity, proactive interference and neurogenesis**

371 So far, available data suggest that better memory retention is associated with reduced

372 cognitive flexibility, and higher cognitive flexibility is associated with worse memory

373 retention. At the same time, adult neurogenesis-mediated forgetting appears to be one of the

374 mechanisms involved in maintaining cognitive flexibility – higher neurogenesis rates

375 decrease memory retention but increase cognitive flexibility, while lower neurogenesis

376 rates seem to increase memory retention but decrease cognitive flexibility (Akers et al.

377 2014; Frankland et al. 2013; Epp, Mera, Kohler,Jesselyn & Frankland, 2016).

378　　　　Existing evidence connecting adult neurogenesis with memory retention and

379　　flexibility comes from a few model species, primarily lab rodents. A big question is

380　　whether this relationship is maintained across species with different life histories or even

381　　across populations experiencing different environments and hence differential selection

382　　pressures. In other words, can we expect that species/populations with higher hippocampal

383　　neurogenesis rates have worse memory retention and higher memory flexibility than

384　　species/populations with lower neurogenesis rates? While there are little data available on

385　　this question, they actually seem to show the opposite. For example, food-caching species

386　　seem to have higher hippocampal neurogenesis rates (Hoshooley & Sherry, 2007) than non-

387　　caching species, but they have better spatial memory (Biegler, McGregor, Krebs, & Healy,

388　　2001; Pravosudov & Roth 2013) and also show more proactive interference/less cognitive

389　　flexibility (Hampton et al. 1998; Lewis & Kamil 2006; Croston et al. 2017). In food-

390　　caching chickadees, birds in harsher winter environments have better spatial memory

391　　(Pravosudov & Clayton 2002; Roth et al. 2012), including longer memory retention (Freas

392　　et al. 2012), but they also have higher hippocampal neurogenesis rates compared to birds

393　　from milder environments (Chancellor et al., 2011; Roth et al. 2012; Freas et al. 2012). At

394　　the same time, chickadees in harsher environments seem to show less cognitive flexibility

395　　compared to chickadees from milder environments (Croston et al. 2017).

396　　　　Indeed, in food-caching species, it appears that better spatial memory is associated

397　　with higher hippocampal neurogenesis rates, but with lower memory flexibility due to

398　　higher levels of proactive interference. We propose memory capacity and load as the

399　　missing, but crucial component in interspecies comparisons (Fig. 1). Higher memory

400　　capacity has been suggested to increase proactive interference (Steinwascher & Meiser,

401　　2016), and it is likely that higher memory load should also increase proactive interference.

402   Species with high demands on memory, such as food-caching species, are likely to

403   have higher memory capacity than non-caching species, as they need to store an enormous

404   number of memories for food cache locations. Chickadee populations in harsher

405   environments also cache more food compared to chickadees from milder winter

406   environments (Roth et al., 2012; Freas et al., 2012), which is likely associated with larger

407   memory load. Higher memory capacity and the need to remember more caches (e.g. more

408   memory load) are likely mediated by a larger hippocampus and a larger total number of

409   hippocampal neurons (Pravosudov & Roth, 2013). However, food-caching species and

410   populations in harsher environments also have higher neurogenesis rates (Hoshooley &

411   Sherry, 2007; Roth et al., 2012; Freas et al., 2012), which is thought to reduce memory

412   retention and increase memory flexibility. We hypothesize that increased hippocampal

413   neurogenesis is a mechanism to reduce negative effects of proactive interference associated

414   with larger memory capacity and load without affecting the retention of relevant memories

415   by mediating forgetting of no longer relevant memories. If cognitive flexibility is

416   advantageous and older memories associated with larger memory load should increase

417   proactive interference and reduce cognitive flexibility, it can be expected that selection

418   should favor some mechanisms that would allow reducing proactive interference while still

419   maintaining long-lasting memories. Rapid neurogenesis-assisted forgetting specifically of

420   no longer relevant memories, such as memories of retrieved caches, may serve as such a

421   mechanism.

422   Species with specialized memory, such as food-caching species, deal with

423   constantly changing information making some memories irrelevant while other memories

424   remain relevant. Considering that selection for memory retention of relevant memories in

425   food-caching species is likely high (e.g. Biegler et al., 2001; Pravosudov & Roth, 2013),

426   irrelevant memories associated with recovered food caches should be rapidly discarded,

427   which should reduce memory load and hence reduce proactive interference. Therefore,

428   higher neurogenesis rates in species or populations that cache more food may serve a

429   critical function of constantly clearing memories of recovered caches. At the same time,

430   higher neurogenesis rates might not fully compensate for higher memory retention and

431   higher memory capacity and load, which might explain why food-caching

432   species/populations with better memory may still have lower memory flexibility and higher

433   levels of proactive interference compared to species/populations with less memory use

434   associated with less caching.

435   Finally, all scatter-hoarding species, such as chickadees and jays, space their food

436   caches so that they are not close together. Such a strategy which was previously argued to

437   reduced cache pilferage (Waite & Reeve, 1993), should also reduce proactive interference,

438   as different caches would be associated with a different set of cues (Croston et al., 2017;

439   Lewis et al., 2013).

440   The extent of memory flexibility and proactive interference might be a trade-off

441   among memory retention, memory capacity and load, and adult neurogenesis rates. Given

442   the same memory capacity/load, memory retention and adult neurogenesis might determine

443   the extent of memory flexibility, but the need for larger memory capacity associated with

444   larger memory load should change the association between memory retention and memory

445   flexibility. To test these ideas, we need more comparative analyses of different

446   species/different populations with different degrees of specialization of memory in

447   combination with experiments manipulating memory load.

448

449 *Memory specialization and better memory retention versus memory generalization and*

450 *higher cognitive flexibility– which is better?*

451 The predictability of the environment and ecology of different species should be the main

452 factors predicting whether cognitive flexibility should be advantageous. When the

453 environment is predictably variable, meaning that a change in the environment is to be

454 expected, animals should benefit the most from being cognitively flexible (Lefebvre et al.,

455 2004; Pravosudov & Roth, 2013). Conversely, completely unpredictable environments that

456 do not provide reliable cues should select against learning altogether (Dunlap & Stephens,

457 2009). Results from cross-generational studies with the fruit fly showed that certain

458 regimens of environmental changes will favor the evolution of learning while others will

459 select against it (Dunlap & Stephens, 2009). At the other extreme, when the environment is

460 very predictable, natural selection should favor the evolution of innate behaviors rather than

461 learning.

462   In between these two extremes, the degree of environmental unpredictability likely

463 determines whether cognitive flexibility would be advantageous. The key here is whether

464 memory retention and cognitive flexibility indeed represent a trade-off. If there is no cost of

465 flexibility it should always be favored, but species and populations do differ in degree of

466 cognitive flexibility (Lefebvre et al. 2004; Croston et al. 2017; Bond, Kamil & Balda,

467 2007), suggesting some costs must exist. If there is a trade-off between memory retention

468 and memory flexibility, different conditions would favor either longer retention or higher

469 flexibility. If the environment changes rapidly and rather unpredictably, the value of

470 previously learned information should be low and the ability to rapidly learn new

471 associations should be favored. If the environment changes more predictably and

472 previously-learned associations retain their value over long periods of time, memory

473   retention should be favored over memory flexibility. For example, in food-caching species,

474   food caches may be used for months after they were originally stored, therefore, memory

475   retention is essential for successful cache retrieval. At the same time, food-caching species

476   seem to exhibit more proactive interference than non-caching species (Hampton et al. 1998)

477   and so appear less cognitively flexible. In contrast, it may be predicted that nomadic species

478   that constantly move should have the highest degree of cognitive flexibility as the value of

479   being able to learn and then discard new information as they move should be higher than

480   retaining past memories which are no longer relevant.

481

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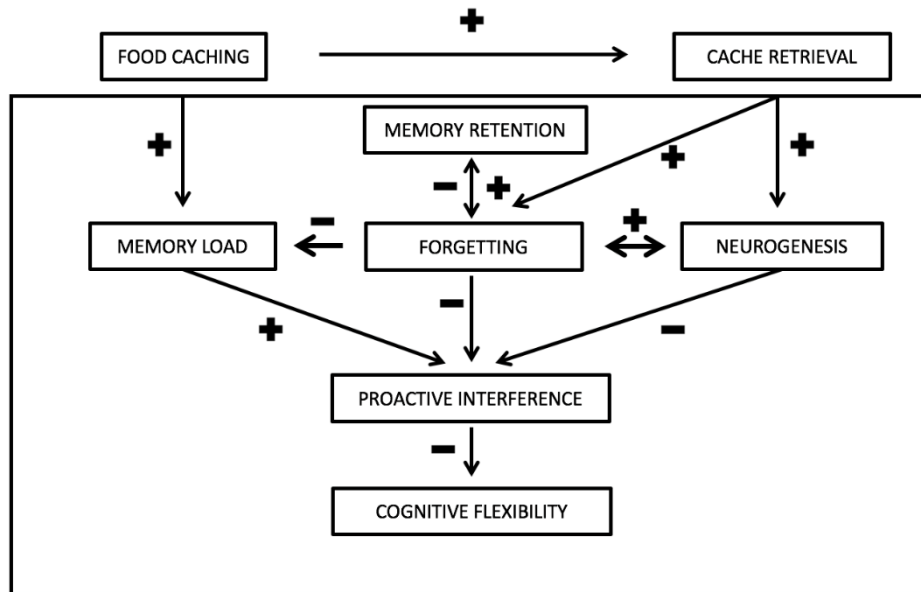
484

485   Figure 1. Hypothesized relationships among memory components thought to influence

486   proactive interference and cognitive flexibility. Memory load is expected to increase

487   proactive interference and reduce cognitive flexibility while forgetting should reduce

488   memory load and to increase flexibility. Higher memory retention may reduce forgetting,

489   while retrieval of memories resulting in no longer relevant information should increase

490   forgetting via increased hippocampal neurogenesis rates. Above the frame is the example

491   of food caching where more food caching increases memory load and provides more

492   opportunities for cache retrieval. More cache retrieval, in turn, should increase forgetting of

493   retrieved caches and so should reduce memory load and reduce interference while also

494   being associated with increased adult hippocampal neurogenesis rates.

495

496   *Future directions*

497   Unfortunately, most existing studies on the relationship among memory retention, memory

498   interference, memory capacity/load, forgetting and neurogenesis are based on just a few

499   model species, such as humans and lab rodents. Historically, psychologists studying animal

500   learning have focused on general principles of learning, which is well suited to study in a

501   few model species. While inter- and intra-specific variation in spatial memory (mainly

502   acquisition and retention) has received considerable attention (e.g. Sherry 2006;

503   Pravosudov & Roth 2013), there is lack of comparative studies investigating such variation

504   in memory flexibility and only a handful of studies attempted comparative analyses of

505   memory flexibility in different species/populations that differ in their life history traits and

506   in their memory needs and use (e.g. Gonzalez et al., 1967; Hampton et al., 1998; Bond et

507   al., 2007; Croston et al., 2017). Most cognitive traits including memory appear to have

508   genetic basis (e.g. Croston et al. 2015), which suggests that they may be affected by natural

509   selection resulting in both inter- and intra-specific variation.

22

510   Comparing multiple species has many challenges considering numerous species

511   differences that may affect cognitive performance (e.g. Pravosudov & Roth 2013) and so it

512   is critical to consider these differences when designing comparative studies. Within-

513   species, population comparisons seem to provide a good alternative which allows

514   comparing cognition in the same species, which is likely to respond similarly to

515   experimental procedures (Pravosudov & Roth 2013). At the same time, comparing

516   populations that may be under different selection pressures should allow better

517   understanding of suggested trade-offs between memory and memory flexibility.

518   Experimental manipulations now possible with wild animals in their natural environment

519   should also allow direct tests for such trade-offs. Small resident birds in particular provide a

520   convenient model to test many of the questions discussed here and link individual variation

521   in cognitive traits to variation in fitness (Croston et al. 2017; Cauchoix 2017). Finally, some

522   traits such as forgetting, might be difficult to measure, but, on the other hand, memory

523   retention can be measured and memory load can also be manipulated experimentally both

524   in the lab and in the field. So, a combination of memory retention, performance in reversal

525   tasks and manipulation of memory load should allow testing the hypotheses discussed here.

526   In the end, however, only comparative analyses in combination with careful

527   experimentation can provide the answers to the following questions:

528   (1) Do memory retention and memory flexibility indeed represent a trade-off? A

529   few existing studies seem to support the idea of such trade-off as a few species compared

530   and studies of lab rodents suggest that animals that retain memories longer do worse in a

531   reversal learning task (less flexible) and animals that do better at reversal learning are

532   worse at memory retention (Akers et al., 2014). Moreover, experimental studies

533   manipulating hippocampal neurogenesis rates also suggest that improving memory

23

534   retention by reducing neurogenesis rates leads to less memory flexibility and improving

535   flexibility by increasing neurogenesis rates leads to reduced memory retention (Akers et al.,

536   2014; Epp et al. 2016). More studies comparing species/populations that differ in either

537   memory retention or memory flexibility are needed to address the generality of this

538   hypothesis and, most importantly, whether potential inter and intra-specific differences in

539   the association between memory retention and memory flexibility have been shaped by

540   natural selection. It is also important to use reversal tasks that do not rely on binary and re-

541   usable choices (e.g. Cauchoix et al. 2017) as such tasks mainly test animals' ability to learn

542   the rules that the rewarding choices always alternate. To test for potential trade-offs

543   between memory retention and flexibility, reversal or serial reversal tasks should involve

544   learning non-repeatable associations during each reversal, which will allow testing both

545   memory retention and memory flexibility as a function of increasing memory load.

546   (2) Does memory load directly affect memory retention, proactive interference and

547   memory flexibility? It is difficult to test for potential differences in memory capacity, but it

548   is possible to experimentally manipulate memory load. Even when we see the suggested

549   relationship between memory retention and memory flexibility, it might potentially be a

550   product of differences in memory experiences and, more specifically, memory load. If

551   individuals have higher memory load (e.g. food-caching species/populations with higher

552   food caching rates), such load might directly affect memory flexibility. By experimentally

553   increasing memory load, it should be possible to test (a) whether larger memory load

554   increases proactive interference and (b) whether such effect is the same or different among

555   different species with potentially different memory demands (e.g. food-caching vs non-

556   caching species). Combining experimentation with memory load and comparative approach

557   using species/populations with different demands on memory should allow for better

558 understanding of the relationship between these memory components and relative

559 contributions of experience and natural selection.

560 (3) Does variation in developmental conditions affect the relationship between

561 memory retention, proactive interference and memory flexibility? There are studies

562 showing that developmental stress negatively affects hippocampal neurogenesis rates

563 throughout life (Lemaire, Koehl, Le Moal, & Abrous, 2000). As adult neurogenesis seems

564 to be involved in forgetting/memory retention/proactive interference relationship, it is thus

565 possible that developmental stress might also affect all memory components.

566 (4) Finally, new research focused on neurogenesis in ecologically-relevant

567 comparisons addressing inter- and intra-specific variation should consider neurogenesis

568 role in forgetting and in reducing proactive interference associated with memory flexibility

569 within the memory retention-memory flexibility paradigm. Measuring neurogenesis rates in

570 all suggested above studies would bring better understanding of how neurogenesis may be

571 involved in mediating memory and memory flexibility trade-offs.

572

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577 *References*
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579 Akers, K. G., Martinez-Canabal, A., Restivo, L., Yiu, A. P., de Cristofaro, A., Hsiang, H.-

580 L., Wheeler, A. L., Guskjolen, A., Niibori, Y., Shoji, H., Ohira, K., Richards, B. A.,

581 Miyakawa, T., Josselyn, S. A., & Frankland, P. W. (2014). Hippocampal

582   neurogenesis regulates forgetting during adulthood and infancy. *Science, 344*, 598-

583   602.

584   Altman, J., & Das, G. (1967). Postnatal neurogenesis in the guinea-pig. *Nature*, *214*, 1098–

585   1101.

586   Altman, J., & Das, G. D. (1965). Post-natal origin of microneurons in the rat brain. *Nature*,

587   *207*, 953–956.

588   Anderson, M. C., & Neely, J. H. (1996). Interference and inhibition in memory retrieval. In

589   E. L. Bjork & R. A. Bjork (Eds.), Memory. Handbook of perception and cognition

590   (pp. 237–332). San Diego, CA: Academic Press.

591   Audet, J.-N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility? *Behavioral*

592   *Ecology*, *28*, 943-947.

593   Badre, D., & Wagner, A. D. (2006). Computational and neurobiological mechanisms

594   underlying cognitive flexibility. *Proceedings of the National Academy of Sciences*

595   *of the United States of America*, *103*, 7186–7191.

596   Barker, J. M., Wojtowicz, J. M., & Boonstra, R. (2005). Where's my dinner? Adult

597   neurogenesis in free-living food-storing rodents. *Genes Brain and Behavior*, *4*, 89-

598   98.

599   Barnea, A., & Pravosudov, V. V. (2011). Birds as a model to study adult neurogenesis:

600   bridging evolutionary, comparative and neuroethological approaches. *European*

601   *Journal of Neuroscience*, *34*, 884-907.

602   Barnea, A., & Nottebohm, F. (1994). Seasonal recruitment of hippocampal neurons in adult

603   free-ranging black-capped chickadees. *Proceedings of the National Academy of*

604   *Sciences of the United States of America*, *91*, 271-221.

Bebus, S. E., Small, T. W., Jones, B. C., Elderbrock, E. K., & Schoech, S. J. (2016).

    Associative learning is inversely related to reversal learning and varies with nestling

    corticosterone exposure. *Animal Behaviour*, *111*, 251–260.

Becker, S. (2005). A computational principle for hippocampal learning and neurogenesis.

    Hippocampus, *15*, 722–738.

Becker, S., MacQueen, G., & Wojtowicz, J. M. (2009). Computational modeling and

    empirical studies of hippocampal neurogenesis-dependent memory: Effects of

    interference, stress and depression. *Brain Research*, *1299*, 45–54.

Biegler, R., McGregor, A., Krebs, J. R., & Healy, S. D. (2001). A larger hippocampus is

    associated with longer-lasting memory. *Proceedings of the National Academy of

    Sciences of the United States of America*, *98*, 6941-6944.

Bjork, R. A. (1970). Positive Forgetting: The noninterference of items intentionally

    forgotten. *Journal of Verbal Learning and Verbal Behavior*, *9*, 255–268.

Bjork, R. A. (1989). Retrieval inhibition as an adaptive mechanism in human memory. In

    H. L. Roediger III & F. I. M. Craik (Eds.), Varieties of memory and consciousness:

    Essays in honour of Endel Tulving (pp. 309–330). Hillsdale: NJ: Erlbaum.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution

    of behavioral flexibility in three species of North American Corvids (*Gymnorhinus

    cyanocephalus*, *Nucifraga columbiana, Aphelocoma californica*). *Journal of

    Comparative Psychology*, *121*, 372-379.

Burghardt, N. S., Park, E. H., Hen, R., & Fenton, A. A. 2012. Adult-born hippocampal

    neurons promote cognitive flexibility in mice. *Hippocampus, 22*, 1795-1808.

627   Cauchoix, M., Hermer, E., Chaine, A. S., Morand-Ferron, J. 2017. Cognition in the field:

628   comparison of reversal learning performance in captive and wild passerines.

629   *Scientific Reports*, 7, 12945.

630   Chambers, R. A., Potenza, M. N., Hoffman, R. E., & Miranker, W. (2004). Simulated

631   apoptosis/neurogenesis regulates learning and memory capabilities of adaptive

632   neural networks. *Neuropsychopharmacology*, *29*, 747–758.

633   Chancellor, L. V., Roth II, T. C., LaDage, L. D., & Pravosudov, V. V. (2011). The effect of

634   environmental harshness on neurogenesis: a large scale comparison. *Developmental*

635   *Neurobiology*, *71*, 246-252.

636   Cheng, K., & Wignall, A. E. (2006). Honeybees (*Apis mellifera*) holding on to memories:

637   response competition causes retroactive interference effects. *Animal Cognition*, *9*,

638   141–150.

639   Crick, C., & Miranker, W. (2006). Apoptosis, neurogenesis, and information content in

640   Hebbian networks. *Biological Cybernetics*, *94*, 9–19.

641   Cristol, D.A., Reynolds, E.B., LeClerc, J.E., Donner, A.H., Farabaugh, C.S. & Ziegenfus,

642   C.W.S. (2003). Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial

643   memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal*

644   *Behaviour*, *66*, 317-328.

645   Croston, R., Branch, C. L., Kozlovsky, D. Y., Dukas, R., Pravosudov, V. V. (2015).

646   Heritability and the evolution of cognitive traits. *Behavioral Ecology*, *26*, 1447-

647   1459.

648   Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L.,

649   & Pravosudov, V. V. (2017). Predictably harsh environment is associated with

650   reduced cognitive flexibility in wild food-caching mountain chickadees. *Animal*

651   *Behaviour*, *123*, 139–149.

652   Dukas, R. (1999). Costs of memory: ideas and predictions. *Journal of Theoretical Biology*,

653   *197*, 41–50.

654   Dukas, R. (2004). Evolutionary Biology of Animal Cognition. *Annual Review of Ecology,*

655   *Evolution, and Systematics*, *35*, 347–374.

656   Dunlap, A. S., & Stephens, D. W. (2009). Components of change in the evolution of

657   learning and unlearned preference. *Proceedings of the Royal Society B: Biological*

658   *Sciences, 276*, 3201–3208.

659   Epp, J. R., Mera, R. S., Kohler, S., Jesselyn, S. A., & Frankland, P. W. (2016).

660   Neurogenesis-mediated forgetting minimizes proactive interference. *Nature*

661   *Communications*, *7*, 10838.

662   Feng, R., Rampon, C., Tang, Y.-P., Shrom, D., Jin, J., Kyin, M., Sopher, B., Martin,G. M.,

663   Kim, S.-H., Langdon, R. B., Sisodia, S. S., & Tsien, J. Z. (2001). Deficient

664   neurogenesis in forebrain-specific Presenlin-1 knockout mice is associated with

665   reduced clearance of hippocampal memory traces. *Neuron*, *32*, 911-926.

666   Festini, S. B., & Reuter-Lorenz, P. A. (2014). Cognitive control of familiarity: directed

667   forgetting reduces interference in working memory. *Cognitive Affective &*

668   *Behavioral Neuroscience*, *14*, 78-89.

669   Frankland, P. W., Köhler, S., & Josselyn, S. A. (2013). Hippocampal neurogenesis and

670   forgetting. *Trends in Neurosciences*, *36*, 497–503.

671   Freas, C., LaDage, L. D., Roth II, T. C., & Pravosudov, V. V. (2012). Elevation related

672   differences in memory and the hippocampus in food-caching mountain chickadees.

673   *Animal Behaviour*, *84*, 121-127.

674   Garthe, A., Behr, J., & Kempermann, G. (2009). Adult-generated hippocampal neurons

675   allow the flexible use of spatially precise learning strategies. PLoS ONE 4: e5464.

676   Gonzalez, R. C., Behrend, E. R., & Bitterman, M. E. (1967). Reversal learning and

677   forgetting in bird and fish. *Science*, *158*, 519–521.

678   Gould, E., Beylin, A., Tanapat, P., Reeves, A. & Shors, T.J. (1999) Learning enhances

679   adult neurogenesis in the hippocampal formation. *Nature Neuroscience*, *2*, 260-265.

680   Guigueno, M. F., MacDougall-Shackleton, S. A., & Sherry, D. F. (2016). Sex and seasonal

681   differences in hippocampal volume and neurogenesis in brood-parasitic brown-

682   headed cowbirds (*Molothrus ater*). *Developmental Neurobiology*, *76*, 1275-1290.

683   Guskjolen, A., Epp, J. R., & Frankland, P. W. (2017). Hippocampal neurogenesis and

684   forgetting. In: The Hippocampus from Cells to Systems, Structure, Connectivity,

685   and Functional Contributions to Memory and Flexible Cognition. D. E. Hannula &

686   M. C. Duff, (Eds), Springer International Publishing.

687   Hampton, R. R., Shettleworth, S. J., & Westwood, R. P. (1998). Proactive interference,

688   recency, and associative strength: comparisons of black-capped chickadees and

689   dark-eyed juncos. *Animal Learning and Behavior*, *26*, 475-485.

690   Hardt, O., Nader, K., & Nadel, L. (2013). Decay happens: The role of active forgetting in

691   memory. *Trends in Cognitive Sciences*, *17*, 111–120.

692   Hoshooley, J. S., & Sherry, D. F. (2007). Greater hippocampal neuronal recruitment in

693   food-storing than in non-food-storing species. *Developmental Neurobiology*, *67*,

694   406-414.

695   Hoshooley, J. S., & Sherry, D. F. (2004). Neuron production, neuron number, and structure

696   size are seasonally stable in the hippocampus of the food-storing black-capped

697   chickadee (*Poecile atricapillus*). *Behavioral Neuroscience*, *118*, 345-355.

698   Hoshooley, J. S., Phillmore, L. S., Sherry, D. F., & MacDougall-Shackleton, S. A. (2007).

699   Annual cycle of the black-capped chickadee: seasonality of food-storing and the

700   hippocampus. *Brain Behavior and Evolution*, *69*, 161-168.

701   Hoshooley, J. S., Phillmore, L. S., & MacDougall-Shackleton, S. A. (2005). An

702   examination of avian hippocampal neurogenesis in relationship to photoperiod.

703   *Neuroreport*, *16*, 987-991.

704   Jacoby, L. L., Hay, J. F., & Debner, J. A. (2001) Proactive interference, accessibility bias,

705   and process dissociations: valid subjective reports of memory. *Journal of*

706   *Experimental Psychology*, *27*, 686-700.

707   Johnson, K. M., Boonstra, R., & Wojtowiccz, J. M. (2010). Hippocampal neurogenesis in

708   food-storing red squirrels: the impact of age and spatial behavior. *Genes, Brain and*

709   *Behavior, 9*, 583-591.

710   Kempermann, G. (2008). The neurogenic reserve hypothesis: what is adult hippocampal

711   neurogenesis good for? *Trends in Neurosciences, 4*, 163-169.

712   Kitamura, T., Saitoh, Y., Takashima, N., Murayama, A., Niibori, Y., Ageta, H., Sekiguchi,

713   M., Sugiyama, H., & Inokuchi, K. (2009). Adult neurogenesis modulates the

714   hippocampus-dependent period of associative fear memory. *Cell*, *139*, 814-827.

715   Kramer, P. J., & Golding, J. M. (1997). Adaptive forgetting in animals. *Psychonomic*

716   *Bulletin & Review*, *4*, 480-491.

717   Kuhl, B. A., & Wagner, A. D. (2009). Forgetting and retrieval. In: Handbook of

718   Neuroscience for the Behavioral Sciences, G. G. Berntson & J. T. Cacioppo, (Eds.),

719   John Wiley & Sons.

720   LaDage, L., Roth II, T. C., & Pravosudov, V. V. (2011). Hippocampal neurogenesis is

721   associated with migratory behavior in adult but not juvenile white-crowned

722   sparrows (*Zonotrichia leucophrys ssp.*). *Proceedings of the Royal Society B:*

723   *Biological Sciences*, *278*, 138-143.

724   LaDage, L. D., Roth II, T. C., Fox, R. A., & Pravosudov, V. V. (2010). Ecologically-

725   relevant spatial memory use modulates hippocampal neurogenesis. *Proceedings of*

726   *the Royal Society B: Biological Sciences, 277*, 1071-1079.

727   Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds

728   and primates. *Brain, Behavior and Evolution*, *63*, 233–246.

729   Lemaire, V., Koehl, M., Le Moal, M., & Abrous, D. N. (2000). Prenatal stress produces

730   learning deficits associated with an inhibition of neurogenesis in the hippocampus.

731   *Proceedings of the National Academy of Sciences of the United States of America*,

732   *97*, 11032-11037.

733   Lewis, J. L., Kamil, A. C., & Webbink, K. E. (2013) Changing room cues reduces the

734   effects on proactive interference in Clark's nutcrackers*, Nucifraga columbiana.*

735   *Journal of Experimental Psychology, 39*, 187-192.

736   Lewis, J. L., & Kamil, A. C. (2006). Interference effects in the memory for serially

737   presented locations in Clark's nutcrackers, *Nucifraga columbiana*. *Journal of*

738   *Experimental Psychology: Animal Behavior Processes*, *32*, 407–418.

739   Martinez-Canabal, A. (2015). Rewiring, forgetting and learning. Commentary: a critical

740   period for experience-dependent remodeling of adult-born neuron connectivity.

741   *Frontiers in Neuroscience. 9*, 298.

742   Mery, F., & Kawecki, T. J. (2003). A fitness cost of learning ability in *Drosophila*

743   *melanogaster*. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 2465–

744   69.

745   Olson, A. K., Eadie, B., Ernst, C., & Christie, B. R. (2006). Environmental enrichment and

746   voluntary exercise massively increase neurogenesis in the adult hippocampus via

747   dissociable pathways. *Hippocampus*, *16*, 250–260.

748   Patel, S. N., Clayton, N. S., & Krebs, J. R. (1997). Spatial learning induces neurogenesis in

749   the avian brain. *Behavioural Brain Research*, *89*, 115–128.

750   Plaçais, P. Y., & Preat, T. (2013). To favor survival under food shortage, the brain disables

751   costly memory. *Science*, *339*, 440–442.

752   Postman, L., Stark, K., & Fraser, J. (1968). Temporal changes in interference. *Journal of*

753   *Verbal Learning and Verbal Behavior*, *7*, 672–694.

754   Pravosudov, V. V., & Roth II, T. C. (2013). Cognitive ecology of food hoarding: the

755   evolution of spatial memory and the hippocampus. *Annual Reviews of Ecology,*

756   *Evolution and Systematics, 44*, 18.1-18.21.

757   Rodriguez, W. a., Borbely, L. S., & Garcia, R. S. (1993). Attenuation by contextual cues of

758   retroactive interference of a conditional discrimination in rats. *Animal Learning &*

759   *Behavior*, *21*, 101–105.

760   Pravosudov, V. V., Roth II, T. C., LaDage, L. D., & Freas, C. A. (2015). Environmental

761   influences on spatial memory and the hippocampus in food-caching chickadees.

762   *Comparative Cognition and Behavior Reviews*, *10*, 25-43.

763   Pravosudov, V. V. & Roth II, T. C. (2013). Cognitive ecology of food hoarding: the

764   evolution of spatial memory and the hippocampus. *Annual Reviews of Ecology,*

765   *Evolution and Systematics, 44*,173-193.

766   Pravosudov, V. V. (2006). On seasonality of food caching behavior in parids: do we know

767   the whole story? *Animal Behavior*, *71*, 1455-1460.

768 Pravosudov, V. V. & Clayton, N. S. (2002). A test of the adaptive specialization

769   hypothesis: population differences in caching, memory and the hippocampus in

770   black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*, *116*, 515-

771   522.

772 Roth II, T.C., LaDage, L. D., Freas, C., & Pravosudov, V. V. (2012). Variation in memory

773   and the hippocampus across populations from different climates: a common garden

774   approach. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 402-410.

775 Sherry, D. F. 2006. Neuroecology. *Annual Reviews in Psychology*, **57**, 167-169.

776 Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of

777   behavioural plasticity. *Animal Behaviour*, *85*, 1004–1011.

778 Steinwascher, M. A., & Meiser, T. (2016). How a high working memory capacity can

779   increase proactive interference. *Consciousness and Cognition, 44*, 130-145.

780 Storm, B. C., & Bjork, R. A. (2016). Do learners predict a shift from recency to primacy

781   with delay? *Memory & Cognition*, *44*, 1204–1214.

782 Strang, C. G., & Sherry, D. F. (2014). Serial reversal learning in bumblebees (*Bombus*

783   *impatiens*). *Animal Cognition*, *17*, 723–734.

784 Swan, A. A., Clutton, J. E., Chary, P. K., Cook, S. G., Liu, G. G., & Drew, M. R. (2014).

785   Characterization of the role of adult neurogenesis in touch-screen discrimination

786   learning. *Hippocampus*, *24*, 1581-1591.

787 van Praag, H., Christie, B. R., Sejnowski, T. J., & Gage, F. H. (1999). Running enhances

788   neurogenesis, learning, and long-term potentiation in mice. *Proceedings of the*

789   *National Academy of Sciences of the United States of America*, *96*, 13427–13431.

790 Waite, T. A., & Reeve, J. D. (1993). Food storage in gray jays: source type and cache

791   dispersion. *Ethology*, *93*, 326-336.

792   Watkins, M. J., & Watkins, O. C. (1976). Cue-overload theory and the method of

793   interpolated attributes. *Bulletin of the Psychonomic Society*, *7*, 289–291.

794   Weisz, V. I., & Argibay, P. F. (2012). Neurogenesis interferes with the retrieval of remote

795   memories: Forgetting in neurocomputational terms. *Cognition*, *125*, 13–25.

796   Wixted, J. T. (2004). The psychology and neuroscience of forgetting. *Annual Review of*

797   *Psychology*, *55*, 235–269.

798   Yau, S. Y., Li, A., & So, K. F. (2015). Involvement of adult hippocampal neurogenesis in

799   learning and forgetting. *Neural Plasticity*, *2015*, 1–13.