

- Deuker, L., Olligs, J., Fell, J., Kranz, T. A., Mormann, F., Montag, C., ... Axmacher, N. (2013). Memory consolidation by replay of stimulus-specific neural activity. *Journal of Neuroscience*, 33(49), 19373–19383.
- Dickey, C. W., Verzhbinsky, I. A., Jiang, X., Rosen, B. Q., Kajfez, S., Stedelin, B., ... Halgren, E. (2022). Widespread ripples synchronize human cortical activity during sleep, waking, and memory recall. *Proceedings of the National Academy of Sciences*, 119(28), e2107797119.
- Gillespie, A. K., Maya, D. A. A., Denovellis, E. L., Liu, D. F., Kastner, D. B., Coulter, M. E., ... Frank, L. M. (2021). Hippocampal replay reflects specific past experiences rather than a plan for subsequent choice. *Neuron*, 109(19), 3149–3163.
- Goode, T. D., Tanaka, K. Z., Sahay, A., & McHugh, T. J. (2020). An integrated index: Engrams, place cells, and hippocampal memory. *Neuron*, 107(5), 805–820.
- Higgins, C., Liu, Y., Vidaurre, D., Kurth-Nelson, Z., Dolan, R., Behrens, T., & Woolrich, M. (2021). Replay bursts in humans coincide with activation of the default mode and parietal alpha networks. *Neuron*, 109(5), 882–893.
- Kaefer, K., Stella, F., McNaughton, B. L., & Battaglia, F. P. (2022). Replay, the default mode network and the cascaded memory systems model. *Nature Reviews Neuroscience*, 23(10), 628–640.
- Kvavilashvili, L., Niedźwieńska, A., Gilbert, S. J., & Markostamou, I. (2020). Deficits in spontaneous cognition as an early marker of Alzheimer's disease. *Trends in Cognitive Sciences*, 24(4), 285–301.
- Liu, Y., Nour, M. M., Schuck, N. W., Behrens, T. E., & Dolan, R. J. (2022). Decoding cognition from spontaneous neural activity. *Nature Reviews Neuroscience*, 23(4), 204–214.
- McCormick, C., Rosenthal, C. R., Miller, T. D., & Maguire, E. A. (2018). Mind-wandering in people with hippocampal damage. *Journal of Neuroscience*, 38(11), 2745–2754.
- O'Callaghan, C., Shine, J. M., Lewis, S. J., Andrews-Hanna, J. R., & Irish, M. (2015). Shaped by our thoughts – a new task to assess spontaneous cognition and its associated neural correlates in the default network. *Brain and Cognition*, 93, 1–10.
- Palmqvist, S., Schöll, M., Strandberg, O., Mattsson, N., Stomrud, E., Zetterberg, H., ... Hansson, O. (2017). Earliest accumulation of β -amyloid occurs within the default-mode network and concurrently affects brain connectivity. *Nature Communications*, 8(1), 1–13.
- Philippi, C. L., Tranel, D., Duff, M., & Rudrauf, D. (2015). Damage to the default mode network disrupts autobiographical memory retrieval. *Social Cognitive and Affective Neuroscience*, 10(3), 318–326.
- Schuck, N. W., & Niv, Y. (2019). Sequential replay of nonspatial task states in the human hippocampus. *Science*, 364(6447).
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1), 11.
- Simons, J. S., Ritchey, M., & Fernyhough, C. (2022). Brain mechanisms underlying the subjective experience of remembering. *Annual Review of Psychology*, 73, 159–186.
- Vaz, A. P., Wittig Jr., J. H., Inati, S. K., & Zaghoul, K. A. (2020). Replay of cortical spiking sequences during human memory retrieval. *Science*, 367(6482), 1131–1134.

Evolutionary mismatch and anomalies in the memory system

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Abstract

In order to understand involuntary autobiographical memories and déjà vu experiences, we argue that it is important to take an evolutionary medicine perspective. Here, we propose that these memory anomalies can be understood as the outcomes of an inevitable design trade-off between type I and type II errors in memory processing.

Barzykowski and Moulin (B&M) offer an excellent synthesis of a wealth of empirical data from a variety of disciplines to simultaneously explain two spontaneous phenomena of the memory

system that have so far eluded satisfying explanation: Involuntary autobiographical memories (IAMS) and déjà vu experiences. Whereas the former are invasive recollections of the personal past, the latter constitute brief experiences of familiarity while simultaneously knowing that the familiarity is false. Like the authors, we think that any theory or account of memory retrieval should account for the apparently pathological or dysfunctional anomalies of the memory system. Furthermore, we find their account extremely compelling, particularly as it places IAMS and déjà vu on a continuum with both involving what Barzykowski and Moulin describe as involuntary cognitions, and our commentary is not at all intended as a criticism of their hypothesis.

Instead, we hope to make use of this opportunity to further advance their proposal by focusing on the ultimate or evolutionary explanation for the phenomena. B&M primarily concentrate on the mechanisms and triggers; providing a convincing proximate explanation for IAMS and déjà vu. However, only in their conclusion do they briefly consider an evolutionary function, suggesting that these memory anomalies can be seen as “the result of a continuously active memory system that automatically and rapidly scans the environment for matching representations”; a suggestion which we would like to expand on. We think there is much promise in the idea that the brain is continually and rapidly scanning the environment for opportune information and attempting to match this to relevant stored representations, a process that sometimes intrudes into conscious awareness. Indeed, it would allow us to explain both IAMS and déjà vu experiences as evolutionary mismatches, phenomena that have received much attention in the evolutionary medicine literature (see Manus 2018; Stearns, 2012; Veit & Browning, 2021). Since our modern environments contain many more stimuli than the ancestral ones in which our memory system evolved, it should not be at all surprising that there can be frequent instances of misfiring, especially when – as in the cases of anomalies such as IAMS and déjà vu experiences – there does not appear to be an immediate fitness cost.

From an evolutionary perspective, there could thus be a straightforward design trade-off in building a costly memory system that has to pay off for the organism to be functional. Since organisms stand to benefit greatly from having pertinent information raised to conscious awareness, while false positives in the form of déjà vu experiences and IAMS have little cost in terms of fitness, it makes sense that evolution would favour the avoidance of type II errors (false negatives such as failing to remember important familiar situations) over type I errors (false positives such as mistakenly thinking that a place is familiar). While it may seem intuitive to think that healthy forms of cognition should not have any anomalies of this sort, to do so would be a failure to recognize that these error rates are inversely related to each other, and thus cannot both be minimized at the same time. There are trade-offs and it is plausible that evolution designed the memory system to prioritize the minimization of type II errors.

Nevertheless, even if there is such a trade-off, that does of course not mean that type II errors are *always* to be preferred over type I errors. As B&M themselves acknowledge, feelings of familiarity can be *pathologically overactive*, where inputs are repeatedly accompanied by feelings of familiarity that Moulin (2013) describes as recollective confabulation. What should we make of these cases that are akin to a permanent déjà vu? From an evolutionary medicine perspective, we should not at all be surprised that neuropathological cases can be found, in which these evolutionary trade-offs are handled in a dysfunctional manner. Indeed, these cases may provide us with the best source of

evidence for understanding how natural selection has dealt with trade-offs in “designing” the human memory system. Importantly, if we want to understand such pathological cases of the mind, it is important to put evolutionary thinking centre stage, since it is only from a Darwinian design stance that we will be able to understand what makes apparent anomalies of the memory system pathological (or for that matter, healthy) (Veit & Browning, 2023). After all, it is precisely in asking for the costs and benefits of different kinds of type I and type II errors that we can begin to understand the memory system as a teleonomic system designed to maximize the fitness of organisms.

Finally, we would like to again reiterate that we believe there to be much promise in the account of B&M. Nevertheless, in order to advance their proposal, we propose that there would be a benefit in studying the anomalies of the memory system framed as type I and type II errors. This could lead to more precise hypotheses that could in turn be tested. Indeed, we may even be able to derive computational models and simulations in order to study these trade-offs and under which environmental conditions there may be fitness advantages to investing in the avoidance of one error over the other. While we have been sceptical of very ambitious attempts to model all phenomena of the mind in terms of free energy minimization or predictive error minimization (Veit & Browning, 2022), this may be a good case for where this framework could legitimately help us to further our understanding of how the brain deals with errors in the memory system and why some errors are evolved features of the architecture of our minds.

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References

- Manus, M. B. (2018). Evolutionary mismatch. *Evolution, Medicine, and Public Health*, 2018(1), 190–191.
- Moulin, C. J. (2013). Disordered recognition memory: Recollective confabulation. *Cortex*, 49(6), 1541–1552.
- Stearns, S. C. (2012). Evolutionary medicine: Its scope, interest and potential. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4305–4321.
- Veit, W., & Browning, H. (2021). Developmental programming, evolution, and animal welfare: A case for evolutionary veterinary science. *Journal of Applied Animal Welfare Science*, 1–13. <https://doi.org/10.1080/10888705.2021.2014838>
- Veit, W., & Browning, H. (2022). Life, mind, agency: Why Markov blankets fail the test of evolution. *Behavioral and Brain Sciences*, 45, E214. <https://doi.org/10.1017/S0140525X22000115>
- Veit, W., & Browning, H. (2023). Hominin life history, pathological complexity, and the evolution of anxiety. *Behavioral and Brain Sciences*, 46, e79. doi: [10.1017/S0140525X22001923](https://doi.org/10.1017/S0140525X22001923)

Involuntary memory signals in the medial temporal lobe

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Abstract

We highlight recent progress in neuroimaging and neuropsychological research on memory mechanisms in the medial temporal lobe that speaks to the involuntary nature of memory retrieval processes. We suggest that evidence from these studies supports Barzykowski and Moulin’s proposal that memory signals involved in experiences of familiarity and déjà vu can be generated in the absence of retrieval intentionality.

We commend Barzykowski and Moulin (B&M) on presenting a theoretical model that considers links between mnemonic experiences that are typically not discussed together in the cognitive-psychology and cognitive-neuroscience literature. We agree with the emphasis on the shared involuntary nature of the memory experiences covered in the model, and the proposed central role that familiarity plays, as summarized in the schematic in Figure 1. At the same time, we feel that this model could be further developed at the mechanistic level through consideration of the functional properties of perirhinal cortex (PrC) in the medial temporal lobe; it is the brain region that has been most closely linked to familiarity assessment in extant research. To this end, we highlight several recent findings, not covered in the target article, that speak to the involuntary mode in which familiarity signals can arise.

PrC has been implicated in familiarity across many functional neuroimaging studies conducted in neurologically healthy participants and in research in individuals with brain damage (Köhler & Martin, 2020; Montaldi & Kafkas, 2022). Although the majority of reports comprising this literature establish a link between PrC and item familiarity in experimental contexts that involve intentional retrieval (e.g., Montaldi, Spencer, Roberts, & Mayes, 2006), a growing body of evidence suggests that this structure also supports involuntary effects of familiarity or fluency that can be observed in the absence of retrieval intentionality. For example, activity in PrC tracks experimental exposure history for verbal and non-verbal stimuli in tasks that show behavioural priming effects (Voss, Hauner, & Paller, 2009; Wang, Ranganath, & Yonelinas, 2014; Yang, McRae, & Köhler, 2023). In related functional magnetic resonance imaging (fMRI) work, we have recently shown that PrC not only tracks recent laboratory exposure, but also degree of judged lifetime exposure to object concepts outside the lab (Duke, Martin, Bowles, McRae, & Köhler, 2017; Yang et al., 2023). Specifically, using a paradigm in which participants made judgements that either required or did not require consideration of lifetime familiarity, we found that fMRI BOLD activity in PrC tracked this memory characteristic regardless of retrieval intentionality. Moreover, observed behavioural performance was also sensitive to lifetime familiarity under conditions in which the latter was task irrelevant (Yang et al., 2023). Overall, such evidence points to PrC as a structure that may support the cue-induced familiarity that is central to involuntary memory retrieval in B&M’s model.

A role for PrC in involuntary memory has also been revealed in research conducted in neurological patients who experience déjà vu