

Comparing integration and contextual binding accounts of memory impairment

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In their recent Opinion (A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nat. Rev. Neurosci.* **20**, 364–375 (2019))¹, Yonelinas et al. reconsidered the standard systems consolidation theory (SSCT)^{2,3} and proposed the contextual binding theory (CBT). For these authors, the long-term development of memory and forgetting can be explained by the way information has been bound during memory formation. Information will be forgotten because different material that occurs in the same context interferes with the item to be learned. The authors propose that CBT can explain better than the SSCT several forgetting effects, including interference effects and retrograde amnesia after post-training hippocampal lesions.

We were pleased to see that this CBT view has much in common with our own ‘integration concept’ (IC), which we introduced to challenge the consolidation–reconsolidation hypothesis^{4,5}. According to the IC, memories, when in an active state (after training or reactivation), become malleable and integrate new information that is present. Depending on the information available at that time, memories can be updated, strengthened (by coherent information), disrupted (by incoherent information resulting from, for example, amnesic treatments or interference) or greatly altered (false memory). We have described evidence^{5,6} showing that performance disruption due to post-training amnesic treatments mainly results from impairments in retrieval that are induced by contextual differences between training and testing.

There are clear convergences between CBT and the IC model. Both accounts challenge the long-held consolidation hypotheses and emphasize a prominent role of environmental context (internal and external) as a major determinant of forgetting. Both accounts note that contextual information presented just before or just after the study event have similar effects on memory, a concept consistent with recent findings^{7–9}.

However, some essential differences should also be noted. Although both IC and CBT claim to explain temporally graded retrograde amnesia, they do not address the same consolidation processes. IC proposes

to explain retrograde amnesia resulting from amnesic treatments delivered during the first minutes following training and thus affecting presumed consolidation–reconsolidation processes. By contrast, CBT suggests an explanation for retrograde amnesia resulting from hippocampal lesions administered days to weeks after training, therefore concerning standard systems consolidation.

Another principal difference between the two frameworks concerns the origin of memory impairment. For CBT, the main source of forgetting is interference between memories that share similar context or content during memory formation. The IC account proposes that forgetting results from a contextual mismatch between acquisition and testing, inducing retrieval difficulties¹⁰. In agreement with the IC, active memories are malleable and integrate any contextual information present. Accordingly, interference is only one source of disruption, among others. As a consequence, the IC model can account for various performance modulations, such as anterograde and retrograde amnesia^{5,6}, interference, false memories, as well as counterconditioning and promnesic effects.

Interestingly, the recent literature seems to converge towards the same aim: revisiting serious shortcomings of older theories of memory impairment. By doing that, CBT and IC both serve to stimulate new conceptions of memory.

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1. Yonelinas, A. P. et al. A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nat. Rev. Neurosci.* **20**, 364–375 (2019).
2. Dudai, Y., Karni, A. & Born, J. The consolidation and transformation of memory. *Neuron* **88**, 20–32 (2015).
3. Frankland, P. W. & Bontempi, B. The organization of recent and remote memories. *Nat. Rev. Neurosci.* **6**, 119–130 (2005).
4. Gisquet-Verrier, P. et al. Integration of new information with active memory accounts for retrograde amnesia: A challenge to the consolidation/reconsolidation hypothesis? *J. Neurosci.* **35**, 11623–11633 (2015).
5. Gisquet-Verrier, P. & Riccio, D. Memory integration: an alternative to the consolidation/reconsolidation hypothesis. *Prog. Neurobiol.* **171**, 15–31 (2018).
6. Gisquet-Verrier, P. & Riccio, D. C. Memory integration as a challenge to the consolidation/reconsolidation hypothesis: similarities, differences and perspectives. *Front. Syst. Neurosci.* **12**, 71 (2019).
7. Cai, D. J. et al. A shared neural ensemble links distinct contextual memories encoded close in time. *Nature* **534**, 115–118 (2016).
8. Rashid, A. J. et al. Competition between engrams influences fear memory formation and recall. *Science* **353**, 383–387 (2016).
9. Redondo, R. L. & Morris, R. G. M. Making memories last: the synaptic tagging and capture hypothesis. *Nat. Rev. Neurosci.* **12**, 17–30 (2011).
10. Tulving, E. & Thomson, D. Encoding specificity and retrieval processes in episodic memory. *Psychol. Rev.* **86**, 739–748 (1973).

Competing interests

The authors declare no competing interests.

Active and effective replay: systems consolidation reconsidered again

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In their recent Opinion article (A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nat. Rev. Neurosci.* **20**, 364–375 (2019))¹, Yonelinas et al. propose that findings often taken as evidence for standard systems consolidation theory (SSCT) can be reinterpreted in a contextual binding (CB) framework. We agree that context is critical for explaining many memory phenomena and that SSCT, as defined, is probably incorrect. We do not advocate for the ideas that all memories become hippocampally independent, that the ones that do come to rely on neocortex retain

the same quality or that the hippocampus does not undergo further learning with replay. Thus, on many counts, we are in agreement. However, we do think that during sleep and offline waking periods, hippocampal–neocortical interactions promote active transformation of memories resulting in increased neocortical engagement, which can usefully be called ‘systems consolidation’, and that some key empirical findings in this area are not predicted by the CB framework.

The CB account posits that replay (in wake or sleep) reflects context-related residual activity, which should tend to diminish with