Hippocampal replay as context-driven memory reactivation

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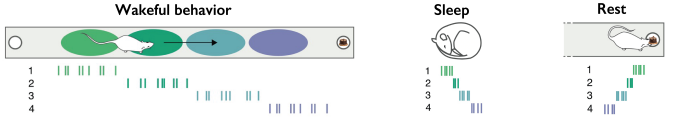
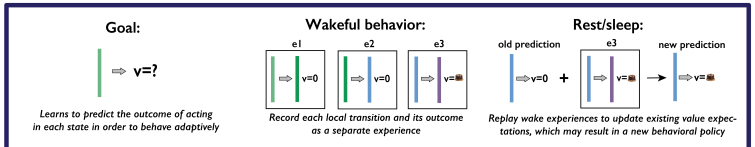
Hippocampal replay recapitulates wake experiences



Spontaneous, sequential hippocampal place cell activity recapitulates the temporal structure of wakeful experience

What is the nature of hippocampal replay?

The reinforcement learning (RL) perspective: Replay as prioritized value updates

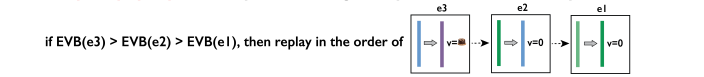


Learns to predict the outcome of acting in each state in order to behave adaptively

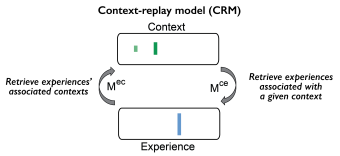
Record each local transition and its outcome as a separate experience

Replay wake experiences to update existing value expectations, which may result in a new behavioral policy

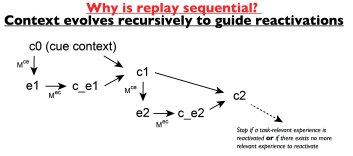
Why is replay sequential? Experiences of high utility to future behaviors are prioritized



Our proposal: Replay as context-driven memory reactivation

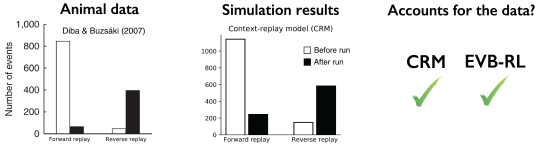


The model associates each experience with its context by updating the two associative matrices at a rate that is modulated by the saliency of an experience



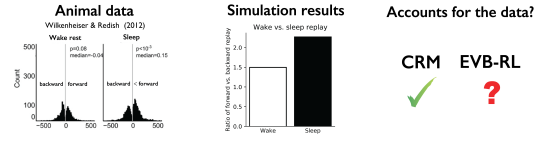
A cue context (i.e., the animal's resting state, or a random state during sleep) evolves to guide sequential, stochastic reactivations. We hypothesize that repeated experience leads to increasing inhibition of task-relevant states in the cue context.

The directionality of replay is context-dependent



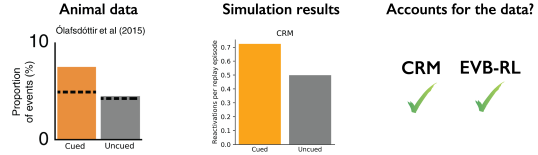
The cue context influences the directionality of replay by biasing which experience will be reactivated first

Increase in forward replay during sleep



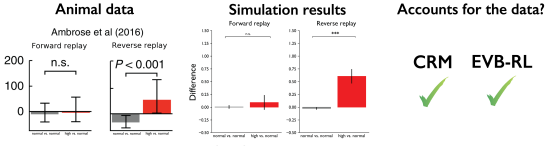
Forward sequences are more likely during sleep relative to wake rest due to higher randomness in what will be reactivated first

Replay over-represents rewarding experiences



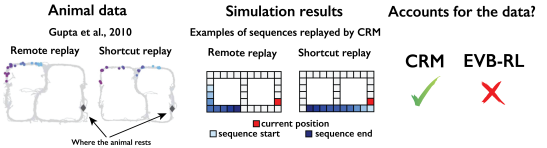
Rewarding experiences are reactivated more frequently due to their elevated encoding rate

Reward uniquely modulates reverse replay



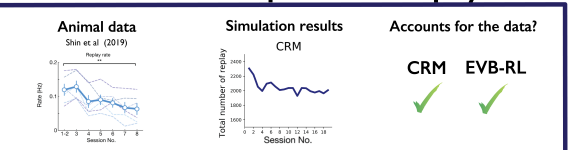
The elevated encoding rate of the final experience allows its encoding context to be retrieved with higher fidelity during replay, leading to increased reverse replay

Replay of remote & novel shortcut trajectories

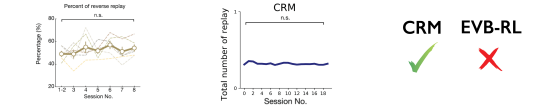


Once a non-local experience is reactivated, retrieval of its encoding context enables CRM to replay coherent non-local trajectories

The influence of experience on replay



Replay frequency decreases due to increasing inhibition of relevant states in the cue through experience



Whereas the EVB-RL model predicts a sharp drop in the proportion backward replay as learning reduces gain

Conclusions

We propose that, during wakefulness, animals associate experiences with the contexts in which they are encoded, in a manner modulated by the salience of each experience. During periods of quiescence, replay emerges when contextual cues trigger a cascade of reactivations driven by the reinstatement of each memory's encoding context, which in turn facilitates memory consolidation.

Our theory unifies numerous replay phenomena, including findings that reinforcement learning models fail to account for.

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