Reverse Replay in the Hippocampus as Optimal Smoothing

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The hippocampus is thought to play an important role in memory and learning. In particular, it has been implicated in the storage and recall of sequential memories such as those represented by place cells during navigation. It has been known for some time that such memories can be reactivated during sleep. A recent study reported that sequential reactivation of stored memories can also occur during awake periods immediately following spatial experience, but the reactivation occurs in a temporally reversed order [1]. It was suggested that such reverse replay of experience may allow reward-based learning of behaviors in a manner consistent with reinforcement learning theories.

We propose an alternative hypothesis for reverse replay in the hippocampus based on the idea of optimal smoothing. Optimal smoothing is an important concept in the fields of probabilistic inference and machine learning. It is an essential ingredient of most statistical algorithms for learning the parameters of a dynamic system. In optimal smoothing, on-line estimates of a random variable that were computed based on input data from time steps 1 to t are later corrected using information from time steps t+1 to T, where T represents the end of the trial. The use of this additional information typically results in a much more accurate estimate for each time step t than the original on-line estimate. The procedure of optimal smoothing involves a forward pass through the data (on-line estimation or "filtering") followed by a backward pass which computes the "smoothed" estimates in temporally reversed order (time steps T, T-1, …, 1). We propose that the reverse replay observed in the CA1 region of the hippocampus are neural correlates of this smoothing process. We suggest that the computation of such smoothed estimates allows accurate unsupervised learning of temporally sequenced information in the hippocampus and the neocortex. We explore the implications of this smoothing hypothesis via simulation studies, and investigate how optimal smoothing could be implemented by hippocampal circuitry.

The hypothesis we have suggested differs from the reinforcement learning interpretation of reverse replay in several ways: (a) it does not require the simultaneous activation and subsequent decay of a reinforcement signal such as dopamine, which is a suggested mechanism for reinforcement learning through reverse replay, (b) it can explain the occurrence of reverse replay in cases where the animal receives no reward, (c) it provides an explanation for why multiple reverse replays typically occur within a given rest period in terms of successive iterations of a statistical learning algorithm (the EM algorithm), and (d) it provides a new framework for understanding unsupervised learning of temporal input sequences in hippocampal and cortical circuitry.

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References
[1] Reverse replay of behavioural sequences in hippocampal place cells during the awake state. D. J. Foster and M. A. Wilson, *Nature* 440:680-683, March 2006.