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Current Opinion in Neurobiology

Oscillations, neural computations and learning during wake and sleep

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Learning and memory theories consider sleep and the reactivation of waking hippocampal neural patterns to be crucial for the long-term consolidation of memories. Here we propose that precisely coordinated representations across brain regions allow the inference and evaluation of causal relationships to train an internal generative model of the world. This training starts during wakefulness and strongly benefits from sleep because its recurring nested oscillations may reflect compositional operations that facilitate a hierarchical processing of information, potentially including behavioral policy evaluations. This suggests that an important function of sleep activity is to provide conditions conducive to general inference, prediction and insight, which contribute to a more robust internal model that underlies generalization and adaptive behavior.

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Current Opinion in Neurobiology 2017, **44**:193–201

This review comes from a themed issue on **Neurobiology of sleep**

Edited by **Yang Dan** and **Thomas Kilduff**

For a complete overview see the Issue and the Editorial

http://dx.doi.org/10.1016/j.conb.2017.05.009

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Introduction

The challenge faced by the brain in perceiving and interpreting the external world is to map a high-dimensional input into neural representations in the form of distributed spiking activity across brain regions, and to then infer causal relationships behind this sensory-driven code. A consequence of this inference is the generation of actions that allow an optimal interaction with the environment in different contexts. Computationally, the complexity of this challenge renders solutions that rely on discriminative methods and lookup tables as rigid and inefficient. Instead, solutions based on probabilistic generative models aim to learn the underlying rules behind external world observations, allowing more general applicability [1,2]. For instance, in the case of spatial exploration, using a lookup table constructed on past navigational experiences, subjects would rely on trial and error exploration to discover different courses when familiar routes are not accessible. By contrast, using a map as a model, subjects could gain in generalization and flexibility because they would be able to devise, evaluate and plan alternative routes without previously having experienced them, as predicted by the cognitive map hypothesis [3,4]. Importantly, knowledge of the spatial layout can have limited value when planning and executing a plan, because a map does not consider conditions and rules that may govern navigation in a given environment. Answering questions such as what paths are available and why they are accessible or not is necessary for an individual to decide how to execute a plan to reach a goal. Hence, incorporating information to answer these *what*, *why* and *how* questions can lead to a more robust model that generates appropriate actions under varying requirements and contexts. Training such a generative model relies on extracting meaningful structure from its inputs to learn statistical representations that can account for the broad set of conditions associated with them [5••]. For neural systems this training could start with the encoding of external information during awake behavior and continue during periods of sleep, resulting in more robust representations that increase behavioral flexibility [6]. Indeed, several studies demonstrate that sleep, in addition to promoting memory consolidation, enables the discovery of implicit rules and insights, which are essential elements for generalization and learning [7]. What computational principles are at work during sleep to facilitate the consolidation of memories while also promoting generalization as well as the inference of causal relationships? While a dialogue between the neocortex and hippocampus has been thought to mediate the systems consolidation of memory and the slow incorporation of statistical regularities into general cortical schemas [8••,9,10], it is unclear whether or how it could also contribute to the training of a generative model that infers causal relationships. In the following sections, we explore the idea that, in the case of spatial navigation, the coordinated neural representations in the hippocampus, neocortex and thalamus during sleep, train a generative model that infers contextual and spatial contingencies, and which can be used during navigation to flexibly select actions to meet contextual conditions.

Predictive coding and neural network representations

Machine learning methods can provide helpful theoretical frameworks for the implementation and training of flexible generative models in the brain. Although deep architectures have enjoyed a recent wave of success [11,12], they largely require explicit external feedback during training, which contrasts with how the brain learns despite the lack of external feedback. Generative networks, by contrast, while typically not structurally deep, can extract statistical patterns in an unsupervised manner [13]. These types of models cast the brain as an inference device that compares predictions generated by an internal model of the world against the ongoing spike train code. Perception, for example, is then a constructive process by which the brain continuously tries to account for its sensations in terms of internally generated expectations or, when a mismatch occurs, updates the model that generates the predictions [14••,15•]. Stochastic recurrent neural networks offer a formal implementation that is consistent with this type of predictive coding because they allow the sequential estimation of probabilistic relationships between time-dependent random variables through generative models. The temporal restricted Boltzmann machine (TRBM) [16•,17], a forerunner to modern recurrent neural networks, offers an intuition of how this process unfolds. The TRBM is composed of a sequence of individual RBMs [18] (Box 1) each of which contains two sets of stochastic binary units. A layer of visible units receives the input to the RBM and is linked to a set of hidden units through connection weights in such a way that the state of the units and the strength of their connections can, through training, extract and encode the statistical regularities of the inputs. Using this computational design as a conceptual framework, even without a specific correspondence with detailed brain anatomy, can provide insights about how neocortical, hippocampal and thalamic networks act together to implement and train a generative model of the world that could be used for flexible behavior. For example, during goal-directed navigation, a subject would benefit from knowing the upcoming spatial layout of the environment and the rules affecting potential choices. In rodents, the spatial component is given by the anticipatory firing of CA1 place cells within cycles of the ongoing theta rhythm (8–12 Hz) in which place cells with partially overlapping receptive fields fire in a temporal sequence that reflects their relative position on the maze [19,20]. These theta sequences represent the upcoming position of the animal and, at decision points, reveal sweeps in the direction of all available options, consistent with an active, constructive evaluation of potential choices [21]. Neocortical areas, including prefrontal and retrosplenial cortices, could represent the rules and actions that ultimately impact the decision of the subject [22–24]. Consistent with this cooperative interaction, prefrontal neurons are selectively phased locked to the hippocampal theta rhythm as subjects approach decision points [25,26]. An additional structure that could assist in coordinating consistent expectations and representations across brain areas is the thalamus, given its role in the expression of intended navigational trajectories in prefrontal cortex and hippocampus [27], its projections to multiple neocortical regions and its potential role in modulating the hippocampal theta oscillation [28,29]. How is this complex network, involving multiple brain regions, trained to support predictive coding?

Training a generative model during awake behavior

Predictive coding relies on correcting errors resulting from comparisons between internal predictions and actual observations. This error, estimated through a process

Box 1 Restricted Boltzmann Machine as a computational model for learning across brain states

The stochastic nature of RBMs allows the estimation of the statistical structure implicit in its inputs in an unsupervised way mimicking the challenge faced by the brain in interpreting the outside world. **(a)** In the RBM formulation, a set of binary visible units interacts directly with incoming stimuli and is linked to a set of binary hidden units; the state of the units and the strength of their connections, represented in a connection matrix, can encode statistical regularities of the input [49]. Computationally, this requires a two-step optimization heuristic known as contrastive divergence: in the first (encoding) step, the visible units are fixed to represent a sample of the external input and the state of the hidden units is obtained and expressed as a hidden vector; in the second (prediction) step, the hidden units are clamped to the recently obtained hidden vector to generate a prediction quantified by casting the value of the visible units into a visible vector. The difference between the joint state of visible and hidden units during the encoding and predictive steps provides an update to the connection matrix so that the internal model better approximates the training sample [29]. Intuitively, the weight between two coactive units will increase in the encoding step, similar to a Hebbian rule, to encourage the hidden units to model the incoming stimulus, whereas the weight between coactive units in the prediction step will decrease to minimize nonspecific correlations. The temporal RBM (TRBM, **(b) top**) is an extension of the RBM that is useful in representing sequential data. At each time step, an RBM corrects its prediction based on the ongoing sample of the external stimulus, and it provides the initial conditions for the hidden units in the immediately following time step. Physiologically, this could correspond to the encoding and retrieval phases associated with the hippocampal theta oscillation; in a given theta cycle, the state of the environment would be communicated through the feedforward connections from entorhinal cortex (EC), allowing for a contrastive divergence-like operation by the recurrent CA3 network, while the expectation of the model, in the retrieval phase, would be reflected by CA1 spiking activity. As an outcome, this process would set up the next expectation of the internal model as navigation unfolds.

The recurrent TRBM (RTRBM, **(b) bottom**) provides a mathematical advantage over the TRBM because, at any given time step, the state of the hidden units is obtained by a deterministic operation based on the state of an intermediary hidden layer (H') at the previous time step along with the current state of the visible layer. Although mapping the exact equivalence between each component of the RTRBM to physiological elements is difficult, the temporal progression of the RTRBM suggests an analogy to the coordinated activity of the hippocampus and neocortex during sleep. Specifically, the notion that temporally coincident reactivation events in both areas, analogous to the state of the intermediary hidden and visible layers at each time step, can be used to infer statistical regularities in their representations that are incorporated into a generative model

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