

Replay in Deep Learning: Current Approaches and Missing Biological Elements

Tyler L. Hayes¹, Giri P. Krishnan², Maxim Bazhenov², Hava T. Siegelmann³, Terrence J. Sejnowski^{2, 4}, Christopher Kanan^{1, 5, 6}

¹Rochester Institute of Technology, Rochester, NY, USA

²University of California at San Diego, La Jolla, CA, USA

³University of Massachusetts, Amherst, MA, USA

⁴Salk Institute for Biological Studies, La Jolla, CA, USA

⁵Paige, New York, NY, USA

⁶Cornell Tech, New York, NY, USA

Keywords: Replay, Sleep, Catastrophic Forgetting

Abstract

Replay is the reactivation of one or more neural patterns, which are similar to the activation patterns experienced during past waking experiences. Replay was first observed in biological neural networks during sleep, and it is now thought to play a critical role in memory formation, retrieval, and consolidation. Replay-like mechanisms have been incorporated into deep artificial neural networks that learn over time to avoid catastrophic forgetting of previous knowledge. Replay algorithms have been successfully used in a wide range of deep learning methods within supervised, unsupervised, and reinforcement learning paradigms. In this paper, we provide the first comprehensive comparison

between replay in the mammalian brain and replay in artificial neural networks. We identify multiple aspects of biological replay that are missing in deep learning systems and hypothesize how they could be utilized to improve artificial neural networks.

1 Introduction

While artificial neural networks now rival human performance for many tasks, the dominant paradigm for training these networks is to train them once and then to re-train them from scratch if new data is acquired. This is wasteful of computational resources, and many tasks involve updating a network over time. However, standard training algorithms, i.e., online error backpropagation, produce catastrophic forgetting of past information when trained from a non-stationary input stream, e.g., incrementally learning new classes over time or most reinforcement learning problems (Abraham and Robins, 2005; Robins, 1995). The root cause of catastrophic forgetting is that learning requires the neural network’s weights to change, but changing weights critical to past learning results in forgetting. This is known as the stability-plasticity dilemma, which is an important problem in deep learning and neuroscience (Abraham and Robins, 2005).

In contrast, humans can continually learn and adapt to new experiences throughout their lifetimes and rarely does learning new information cause humans to catastrophically forget previous knowledge (French, 1999). In the mammalian brain, one mechanism used to combat forgetting and facilitate consolidation is replay - the reactivation of past neural activation patterns¹ (McClelland et al., 1995; Kumaran et al., 2016; McClelland et al., 2020). Replay has primarily been observed in the hippocampus, which is a brain structure critical for consolidating short-term memory to long-term memory. Replay was first noted to occur during slow-wave sleep, but it also occurs during Rapid Eye Movement (REM) sleep (Louie and Wilson, 2001; Eckert et al., 2020; Kudrimoti et al., 1999) and while awake, potentially to facilitate the retrieval of recent memories (Walker and Stickgold, 2004).

¹For simplicity, we use replay to refer to both reactivation and replay. In the neuroscience literature, replay typically refers to the reactivation of a sequence of *more than one* neural patterns in the same sequence they occurred during waking experience, but here we define it as the reactivation of *one or more* neural patterns.

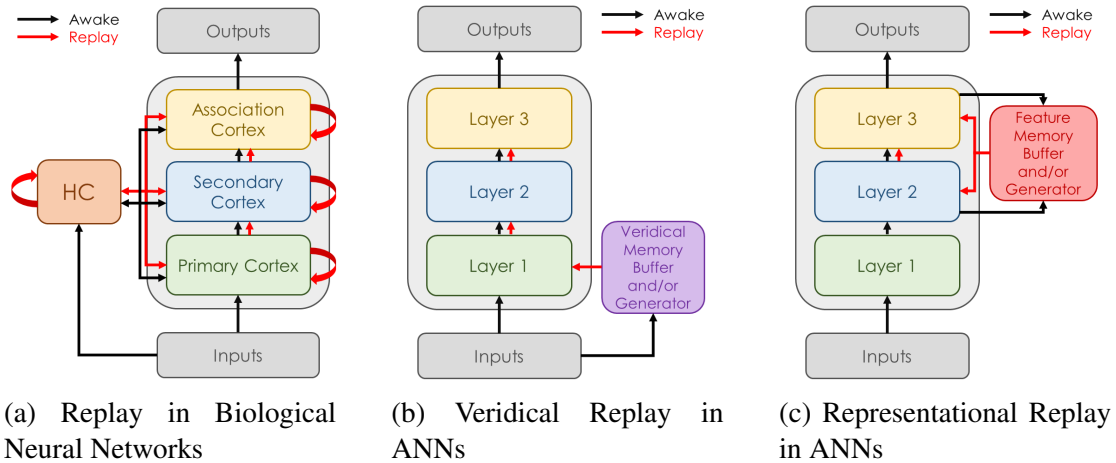


Figure 1: High-level overview of the flow of learning activity during awake and replay stages in biological networks versus artificial neural networks (ANNs). While replay occurs in several brain regions both independently and concurrently, replay in most artificial implementations occurs concurrently from a single layer. While the hippocampal complex (HC) can be used for both replay and inference in biological networks, the memory buffers in artificial replay implementations are mostly used to train the neural network that makes predictions. Figures (b) and (c) are examples of replay in an ANN with 3 hidden layers. For networks with more layers, the layer for representational replay can be chosen in a variety of ways (see text).

In artificial networks, the catastrophic forgetting problem during continual learning has been successfully addressed by methods inspired by replay (Rebuffi et al., 2017; Castro et al., 2018; Wu et al., 2019a; Hou et al., 2019; Hayes et al., 2020). In the most common implementation, replay involves storing a subset of previous veridical inputs (e.g., RGB images) and mixing them with more recent inputs to update the networks (Rebuffi et al., 2017; Castro et al., 2018; Wu et al., 2019a; Hou et al., 2019; Andrychowicz et al., 2017; Schaul et al., 2016; Lesort et al., 2019; Wu et al., 2018; Draelos et al., 2017). This preserves representations for processing previous inputs while enabling new information to be learned. In contrast, the brain replays highly processed representations of past inputs, e.g., those stored within the hippocampus (Teyler and Rudy, 2007), and a similar approach has been used to enable continual learning for artificial networks in some recent works that replay high-level feature representations (Hayes et al., 2020; Iscen et al., 2020; Caccia et al., 2019; Pellegrini et al., 2019; van de Ven et al., 2020). While this is closer to biology, many facets of replay in biology have not been incorporated into artificial networks, but they could potentially

Table 1: High-level overview of replay mechanisms in the brain, their hypothesized functional role, and their implementation/use in deep learning.

REPLAY MECHANISM	ROLE IN BRAIN	USE IN DEEP LEARNING
Replay includes contents from both new and old memories	Prevents forgetting	Interleave new data with old data to overcome forgetting
Only a few selected experiences are replayed	Increased efficiency, weighting experiences based on internal representation	Related to subset selection for what should be replayed
Replay can be partial (not entire experience)	Improves efficiency, allows for better integration of parts, generalization, and abstraction	Not explored in deep learning
Replay observed at sensory and association cortex (independent and coordinated)	Allows for vertical and horizontal integration in hierarchical memory structures	Some methods use representational replay of higher level inputs or feature maps
Replay modulated by reward	Allow reward to influence replay	Similar to reward functions in reinforcement learning
Replay is spontaneously generated (without external inputs)	Allows for all of the above features of replay without explicitly stored memories	Some methods replay samples from random inputs
Replay during NREM is different than replay during REM	Different states allow for different types of manipulation of memories	Deep learning currently focuses on NREM replay and ignores REM replay
Replay is temporally structured	Allows for more memory combinations and follows temporal waking experiences	Largely ignored by existing methods that replay static, uncorrelated inputs
Replay can happen in reverse	Allow reward mediated weighting of replay	Must have temporal correlations for reverse replay
Replay is different for novel versus non-novel inputs	Allows for selective replay to be weighted by novelty	Replay is largely the same independent of input novelty

improve generalization, abstraction, and data processing. A high-level depiction of the differences between biological and artificial replay is shown in Fig. 1.

In this paper, we first describe replay’s theorized role in memory consolidation and retrieval in the brain, and provide supporting evidence from neuroscience and psychology studies. We also describe findings in biology that deviate from today’s theory. Subsequently, we discuss how replay is implemented to facilitate continual learning in artificial neural networks. While there have been multiple reviews of replay in the brain (Tingley and Peyrache, 2020; Ólafsdóttir et al., 2018; Pfeiffer, 2020; Foster, 2017; Robertson and Genzel, 2020) and reviews of continual learning in artificial

networks (Kemker et al., 2018; Parisi et al., 2019; De Lange et al., 2019; Belouadah et al., 2020), we provide the first comprehensive review that integrates and identifies the gaps between replay in these two fields. While it is beyond the scope of this paper to review everything known about the biology of replay, we highlight the salient differences between known biology and today’s machine learning systems to help biologists test hypotheses and help machine learning researchers improve algorithms. An overview of various replay mechanisms in the brain, their hypothesized functional role, and their implementation in deep neural networks is provided in Table 1.

2 Replay in Biological Networks

Memory in the brain is the process of encoding, storing, and retrieving information. Encoding involves converting information into a format that can be stored in short-term memory, and then a subset of short-term memories are consolidated for long-term storage. Consolidation is a slow process that involves the integration of new memories with old (McGaugh, 2000). Splitting learning into short-term and long-term memory allows the brain to efficiently solve the stability-plasticity problem. The consolidation phase is used for long-term storage of declarative, semantic, and procedural memories (Rasch and Born, 2013; Born, 2010; Stickgold, 2005, 2012).

Consolidation occurs during periods of rest or sleep, where spiking activity during replay initiates long-term changes in synapses through activity dependent plasticity processes. Consolidation is well understood for declarative and semantic memory, which depend on the hippocampus. Bilateral removal of the hippocampus results in anterograde amnesia and the inability to form new semantic memories (Nadel and Moscovitch, 1997). The primary input to the hippocampus is the entorhinal cortex, which receives highly processed information from all sensory modalities and the prefrontal cortex. While the hippocampus allows for the quick assimilation of new information, medial prefrontal cortex is used for long-term storage of memories and generalization (Bontempi et al., 1999). These generalization capabilities are a result of medial prefrontal cortex using a slower learning rate and densely encoding memories with overlapping representations, whereas the hippocampus uses a faster learning rate in

conjunction with sparsity and indexing mechanisms (Teyler and Rudy, 2007). Hebbian learning and error-driven schemes are used by both the hippocampus and medial prefrontal cortex (O'Reilly and Rudy, 2001). Initially, the hippocampus is used to retrieve new memories, but over time medial prefrontal cortex is instead used for retrieval (Kitamura et al., 2017). Results from (Kitamura et al., 2017) suggest that when new memories are created, neurons are allocated in both the hippocampus and medial prefrontal cortex, with unused neurons in the hippocampus engaged immediately for formation and neurons in medial prefrontal cortex being epigenetically 'tagged' for later storage (Lesburguères et al., 2011; Bero et al., 2014). This switch from hippocampus to cortex occurs over a period of several days with several episodes of sleep, however, it can take months or even years to make memories completely independent of the hippocampus. Replay during sleep determines which memories are formed for long-term storage.

The complementary learning systems (CLS) theory describes long-term memory consolidation based on the interplay between the hippocampus and the neocortex (McClelland et al., 1995; Kumaran et al., 2016). In this framework, the hippocampus and cortex act complimentary to one another. The hippocampus quickly learns short-term instance-level information, while the cortex learns much more slowly and is capable of better generalization. The CLS theory (McClelland et al., 1995; Kumaran et al., 2016) also suggests that the brain generalizes across a variety of experiences by retaining episodic memories in the hippocampal complex and consolidating this knowledge to the neocortex during sleep.

Consolidation of hippocampus independent short-term memory, such as emotional and procedural memory, is also enhanced by sleep (McGaugh, 2000; Hu et al., 2006; Payne et al., 2008; Wagner et al., 2001). Sleep improves motor sequence learning (Walker et al., 2005, 2002a), motor adaptation (Stickgold, 2005), and goal-related sequence tasks (Albouy et al., 2013; Cohen et al., 2005). Learning motor tasks involves many brain regions including motor cortex, basal ganglia, and hippocampus (Debas et al., 2010). While some improvement in sequential motor tasks may arise from the hippocampal contribution during sleep (King et al., 2017), improvement in motor adaptation tasks does not involve the hippocampus (Debas et al., 2010). Sleep has also been

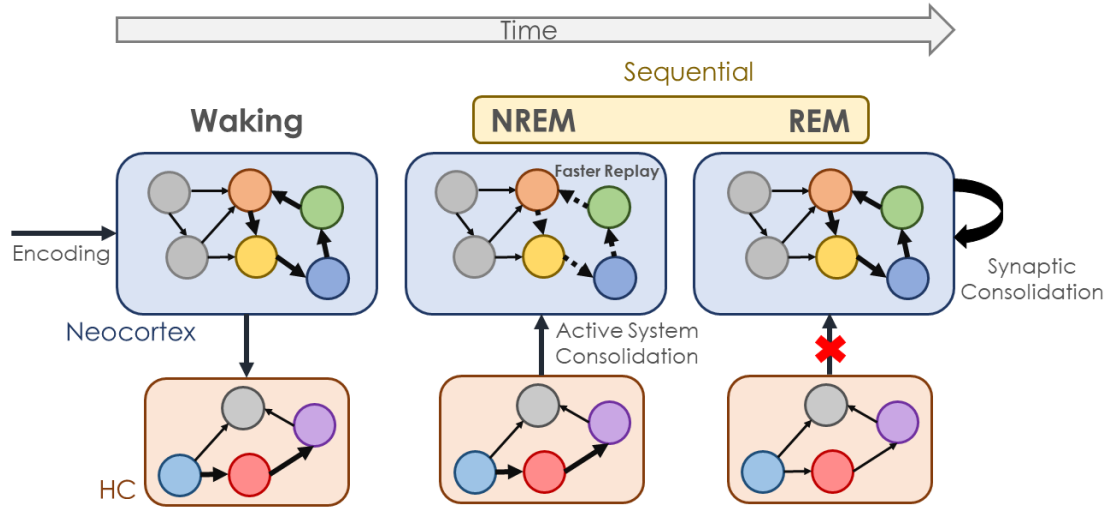
shown to prevent interference between procedural and declarative tasks (Brown and Robertson, 2007), suggesting a role for sleep in preventing interference during consolidation of different memory types.

Different sleep stages have distinct roles in memory consolidation. Non-rapid eye movement (NREM) sleep is strongly associated with consolidation of declarative memory (Diekelmann, 2014; Walker and Stickgold, 2010). In contrast, rapid eye movement (REM) sleep promotes the organization of internal representations (Dumay and Gaskell, 2007; Haskins et al., 2008; Bader et al., 2010; Tibon et al., 2014), abstraction (Gómez et al., 2006; Wagner et al., 2004; Smith and Smith, 2003; Djonlagic et al., 2009; Cai et al., 2009; Lewis et al., 2018; Durrant et al., 2015), and protects against interference between memories (McDevitt et al., 2015). In motor tasks, NREM is associated with the improvement of simple sequential tasks, while REM promotes the consolidation of complex motor tasks (King et al., 2017). REM also selectively promotes consolidation of emotional memories (Baran et al., 2012; Wagner et al., 2001). This collection of evidence suggests NREM is associated with transfer and storage of recent experiences and REM is associated with organizing internal representations. This also coincides with NREM occurring more during early parts of night sleep, when transfer occurs, followed by REM sleep occurring predominately during the later part of night sleep, when integration and higher order memory manipulations occur. This is illustrated in Fig. 2.

2.1 Replay Reflects Recent Memories

Since synaptic plasticity mechanisms that result in long-term changes are activity dependent (Bi and Poo, 1998; Markram et al., 1997; Abbott and Nelson, 2000), replay during sleep plays a critical role in long-term memory consolidation.

The first evidence of replay in the hippocampus was observed in the firing patterns of pairs of neurons (Pavlides and Winson, 1989; Wilson and McNaughton, 1994). In these studies, the firing patterns of ‘place cells’ in the hippocampus were measured during sleep. Since place cells are known to spike when the animal is in a particular location (O’Keefe and Nadel, 1978), it is possible to study neurons that are active during both sleep and recent waking experiences. A strong correlation was observed



(a) Depiction of the contributions of replay to memory formation and consolidation during waking, NREM, and REM stages.

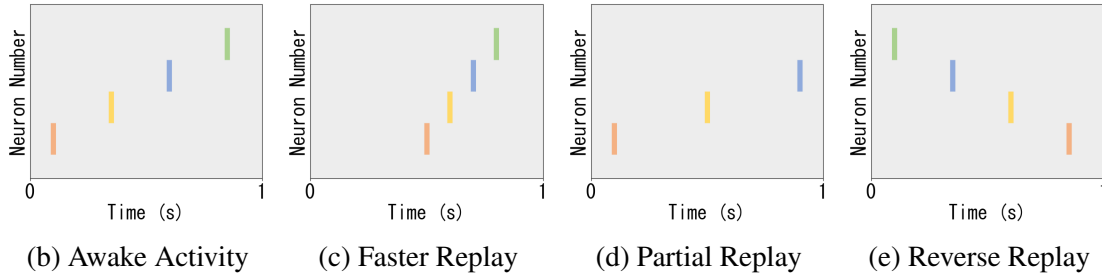


Figure 2: (a) Visualization of the contribution of replay in the hippocampal complex (HC) and the neocortex during different stages. Spike traces of neocortical outputs during (a) awake activity, (b) faster replay (NREM), (c) partial replay (NREM and REM), and (d) reverse replay (reinforcement learning). Note that activity during REM has been observed to be similar to that during waking experiences.

between the firing rates of place cell neurons during sleep to those observed during the waking task (Pavlides and Winson, 1989; Wilson and McNaughton, 1994). Such replay of recent learning has been replicated across several studies (Louie and Wilson, 2001; Davidson et al., 2009) and in other brain regions (Peyrache et al., 2009; Ji and Wilson, 2007a). Subsequent studies focus on the relative timing of different neurons, and identified a similarity in the temporal order of spiking between awake experiences and sleep (Louie and Wilson, 2001; Ji and Wilson, 2007a).

Replay of recent memories in hippocampus decays over time, with the progressive reduction of correlations in the firing of neurons with recent experience over several sleep cycles (Nádasy et al., 1999). There is also a reduction in the strength of replay during awake rest across days (Karlsson and Frank, 2009). The decline in replay of

recent experiences was shown to occur relatively fast in hippocampus and prefrontal cortex, i.e., within a matter of hours (Kudrimoti et al., 1999; Tatsuno et al., 2006). The decline of replay in recent experiences during sleep is followed by the resetting of hippocampal excitability during REM sleep (Grosmark et al., 2012), which may allow the hippocampus to encode new memories.

Replay of recent memories has also been observed in brain regions outside of the hippocampus. For example, the prefrontal cortex shows firing patterns similar to recent learning that are time-compressed (Euston et al., 2007; Peyrache et al., 2009). Coordinated replay between hippocampus and visual cortex has also been observed (Ji and Wilson, 2007b), which provides direct evidence for the transfer of memories from hippocampus to cortex. Recent procedural memories also result in the replay of task related activity during sleep. Scalp recordings during sleep resemble activity during recently learned motor tasks (Schönauer et al., 2014). Spiking activity from motor cortex during NREM sleep has firing patterns that are similar to recent learning (Ramanathan et al., 2015; Gulati et al., 2017, 2014). Further, replay during sleep was essential for solving the credit assignment problem by selectively increasing task related neuron activity and decreasing task unrelated neuron activity following sleep (Gulati et al., 2017). Taken together, these findings suggest recent memories are replayed by many different brain regions during sleep, some of which may relate to hippocampus, while others appear to originate locally or through other brain regions.

2.2 Selective Replay Enables Better Memory Integration

Replay does not exactly replicate activity during waking experiences. An explicit demonstration of this effect was shown in a two choice maze task, where replay in rats corresponded to paths that were experienced and shortcuts that were never experienced (Gupta et al., 2010). More recently, replay during sleep in the hippocampus and prefrontal cortex corresponded to separate activation of movement related and movement independent representations (Yu et al., 2017). Likewise, commonly used methods for analyzing replay, e.g., template matching, principal component analysis, and independent component analysis, have shown high similarity, but not an exact match,

between activation patterns during waking and sleep (Lee and Wilson, 2002; Louie and Wilson, 2001; Peyrache et al., 2009).

Selective and partial replay are, in part, responsible for why replay is not an exact reconstruction of waking experience. Since sleep is time limited as compared to the time required to replay *all* memories related to recent experiences, replaying only selected experiences can be more efficient for consolidation. Which experiences are selected for replay remains an open question. It was suggested that old experiences that overlap with new memories are in the most danger of being damaged by new learning and are preferentially replayed (McClelland et al., 2020). Further, only certain sub-parts of the selected experiences are replayed. Such partial replay allows relevant memories with shared components to be blended, which could result in improved generalization. This was demonstrated in a recent experiment involving rats in various tasks, where coordinated partial replay of hippocampal and prefrontal cortical neurons represented generalization across different paths (Yu et al., 2018). MEG studies in humans after training on tasks involving sequences with overlapping structure had activity evident of partial replays that resulted in generalization (Liu et al., 2019b). Partial replay has also been proposed to build cognitive schemata (Lewis and Durrant, 2011). Thus, partial replay provides a mechanism for higher order memory operations, which is not a simple repetition of past experience.

Rewards received during tasks are strong modulators of replay during sleep. The temporal order of replay can be reversed when it is associated with a reward, and the strength of this reversal is correlated with the reward magnitude (Ambrose et al., 2016). Reverse replay can be explained based on a form of spike time dependent synaptic plasticity (STDP), which allows for symmetric connections in both directions following sequential activation with rewards at the end of the sequence (Pfeiffer, 2020). A series of human experiments further suggest that selective and partial replay in tasks involving reward allow humans to perform generalization and model-based reinforcement learning (Momennejad, 2020), which has inspired several algorithms in machine learning (see (Cazé et al., 2018) for a review). Another important function of selective and partial replay is in planning. Replay is shown to include activity sampled from past experiences as well as novel activity that corresponds to future possibilities (Johnson

and Redish, 2007) and random movements in place cells (Stella et al., 2019). Experimental and theoretical studies have identified partial replay as a potential mechanism for exploring possible routes or facilitating goal-directed navigation (Foster and Knierim, 2012; Pfeiffer and Foster, 2013). For example, partial replay corresponded to different locations in the environment that could facilitate the reconstruction of unexplored paths and novel future trajectories (Ólafsdóttir et al., 2015, 2018).

Since reverse replay begins with the state of the reward and spike sequences trace backwards, it has been proposed to be similar to backward planning from the goal in Markov decision processes (Foster, 2017). Thus, reverse replay could be an efficient way of estimating state values, which are critical in reinforcement learning.

2.3 Replay Generation and Coordination Across Brain Regions

The exact mechanism for the spontaneous origin of replay during sleep and resting periods is not well understood. During sleep, there is a large change in the neuromodulatory tone for each sleep state across the entire brain (Brown et al., 2012; McCormick, 1992; Watson et al., 2010). Neuromodulatory levels determine a neuron’s excitability and the strength of its synaptic connections. During NREM sleep, due to a reduction in acetylcholine and monoamine levels, there is an overall reduction in neuron excitability and an increase in excitatory connections. Further, increased extracellular GABA during NREM suggests an increase in inhibition during this state. The reduced excitability and heightened synaptic connections result in spontaneous activity during sleep (Olcese et al., 2010; Krishnan et al., 2016). This reflects patterns of synaptic connectivity between neurons rather than the intrinsic state of neurons. Reactivation has also been observed in computational models of attractor networks (Shen and McNaughton, 1996), where random activations initiate attractor dynamics that result in the replay of activity that formed the attractor. If synaptic changes reflect previous learning, such as a particular group of neurons co-activating or a sequential activation of neurons, then the activity generated during sleep follows or replays the activity from learning. This has been demonstrated in several studies involving recurrently connected thalamocortical networks (Wei et al., 2016, 2018; González et al., 2020). The studies demonstrated

that replay helps to avoid interference between competing memories and results in a synaptic connection that reflects the combination of previous tasks (Golden et al., 2020; González et al., 2020).

An important characteristic of sleep is the synchronization of firing across neurons that leads to oscillations (e.g., oscillations in the local field potential or EEG signals). Replay during sleep was shown to co-occur with sleep oscillations. NREM sleep is characterized by several well-defined types of oscillations, found across a wide range of species from reptiles to humans, including sharp wave ripples (100-200 Hz) in the hippocampus (Buzsáki et al., 1992), spindles (7-14 Hz) (Morison and Dempsey, 1941) and slow (< 1 Hz) oscillations (Steriade et al., 2001, 1993) in the thalamocortical network (Bazhenov and Timofeev, 2006). Numerous studies have demonstrated that replay in the hippocampus is linked to the occurrence of sharp-wave ripples (Nádasdy et al., 1999; Foster and Wilson, 2006; Davidson et al., 2009; Peyrache et al., 2009; Buzsáki, 2015). In the cortex, replay occurs during spindles and active states of slow oscillations (Ramanathan et al., 2015). Indeed, oscillatory activities during NREM stage 2 sleep, including sleep spindles and slow waves, are strongly correlated with motor sequence memory consolidation (Nishida and Walker, 2007; Barakat et al., 2013).

There is evidence for the coordination between oscillations across the cortex and hippocampus (Battaglia et al., 2004; Sirota et al., 2003; Mölle et al., 2006; Siapas and Wilson, 1998), suggesting that sleep rhythms can mediate the coordinated replay between brain regions. The nesting of ripples, spindles, and slow oscillations was reported in vivo (Staresina et al., 2015) and demonstrated in large-scale biophysical models (Sanda et al., 2021). Coordinated replay is supported by simultaneous recordings from hippocampus and neocortex (Ji and Wilson, 2007a). Taken together, these evidences strongly suggest that replay in the neocortex is modulated by the hippocampus during sleep. Such coordination is critical for the transfer of recent memories from hippocampus to cortex and also across cortical regions. This coordination leads to the formation of long-range connections and promotes associations across memories and modalities.

Properties of sleep oscillations influence replay and synaptic plasticity during sleep. The frequency of spiking during spindles is well suited for initiating spike timing de-

pendent synaptic plasticity (STDP) (Sejnowski and Destexhe, 2000). Both spindles and slow oscillations demonstrate characteristic spatio-temporal dynamics (Muller et al., 2016) and its properties determine synaptic changes during sleep (Wei et al., 2016).

2.4 Open Questions About Replay

There are several open questions about replay in biological networks that are far from being well understood. One of them is about the origin and functions of replay during REM sleep. REM sleep has been shown to play at least three intertwined roles (Walker and Stickgold, 2010): 1) it *unitizes* distinct memories for easier storage (Haskins et al., 2008; Bader et al., 2010; Tibon et al., 2014; Kuriyama et al., 2004; Ellenbogen et al., 2007), 2) it *assimilates* new memories into existing networks (Walker et al., 2002b; Stickgold et al., 1999; Dumay and Gaskell, 2007), and 3) it *abstracts* high-level schemas and generalizations to unlearn biased or irrelevant representations (Gómez et al., 2006; Wagner et al., 2004; Smith and Smith, 2003; Djonlagic et al., 2009; Cai et al., 2009; Lewis et al., 2018; Durrant et al., 2015). REM sleep also facilitates creative problem-solving (Lewis et al., 2018; Baird et al., 2012; Cai et al., 2009).

While the majority of replay studies are from NREM sleep, some studies have shown replay during REM sleep (Louie and Wilson, 2001; Eckert et al., 2020; Kudrimoti et al., 1999). Early studies did not find a correlation in firing patterns during REM, which had been found in NREM sleep (Kudrimoti et al., 1999). However, (Louie and Wilson, 2001) identified replay during REM in hippocampal place cells similar to NREM. In the case of motor skill learning, reactivation was observed during both REM and NREM sleep. Moreover, replays during REM and NREM are interlinked, since replay during REM is correlated with replay during NREM from the previous night (Eckert et al., 2020). REM sleep was implicated in pruning newly-formed post-synaptic dendritic spines in the mouse motor cortex during development and motor learning and was also shown to promote the survival of new, learning-induced, spines that are important for the improvement of motor skills (Li et al., 2017). Together, these studies point to the important but still poorly understood role of REM sleep in memory and learning and suggest that the repetition of NREM and REM stages with different

neuromodulatory states are critical for memory consolidation.

What is the meaning of replayed activity? While in some cases the replay faithfully replicates activity learned during awake, many evidences suggest that the content of replay is more than just a simple combination of past activities. As the brain learns new memories that may potentially try to allocate synaptic resources belonging to the old memories, sleep may not simply replay previously learned memories to avoid forgetting. Instead, sleep may change representations of the old memories by re-assigning different subsets of neurons and synapses to effectively orthogonalize memory representations and allow for overlapping populations of neurons to store multiple competing memories (González et al., 2020).

One of the outstanding questions about replay involves the selection of replayed activity. As highlighted in previous works (McClelland et al., 2020), given the limited time period of sleep, only a subset of memories are selected for replay during sleep. This suggests that the neural activity during sleep is selected to maximize consolidation, while simultaneously preventing forgetting. Machine learning algorithms could optimize directly for which old memories to be replayed during consolidation to long-term memory; these ideas could inform neuroscience research. While there are major differences between the nature of activity in artificial and spiking networks, machine learning inspired replay methods could still provide insights about neural activity selection during sleep replay.

3 Replay in Artificial Networks

When a deep neural network can be trained in an offline setting with fixed training and testing datasets, gradient descent can be used to learn a set of neural weights that minimize a loss function. However, when the training set evolves in a non-stationary manner or the agent learns from a sequence of experiences, gradient descent updates to the network cause *catastrophic forgetting* of previously learned knowledge (McCloskey and Cohen, 1989; Abraham and Robins, 2005). This forgetting occurs because parametric models, including neural networks, assume that data is independent and identically distributed (iid). In offline settings, models can simulate the notion of iid experiences by

shuffling data. However, in continual learning settings, the data stream is evolving in a non-iid manner over time, which causes catastrophic forgetting of previous knowledge.

Further, offline machine learning setups are unable to continually learn new data since they assume there are distinct periods of training versus evaluation, that the training and testing data come from the same underlying data distribution, and that all of the training data is available at once. When these assumptions are violated, the performance of neural networks degrades. The broad field of *lifelong machine learning* seeks to overcome these challenges to continually train networks from evolving non-iid data streams. In addition to overcoming catastrophic forgetting, lifelong learning agents should be capable of using previous knowledge to learn similar information better and more quickly, which is known as forward knowledge transfer. This survey and much of the existing lifelong learning literature have focused on overcoming catastrophic forgetting using replay, however forward knowledge transfer is also an important aspect of lifelong learning that has received little attention (Chaudhry et al., 2018; Lopez-Paz and Ranzato, 2017), and should be studied in more detail.

Moreover, catastrophic forgetting occurs due to the stability-plasticity dilemma, which requires networks to keep weights of the network stable in order to preserve previous knowledge, but also keep weights plastic enough to learn new information. Three main types of methods for mitigating forgetting have been proposed (Parisi et al., 2019; Kemker et al., 2018; De Lange et al., 2019): 1) regularization schemes for constraining weight updates with gradient descent (Kirkpatrick et al., 2017; Aljundi et al., 2018; Zenke et al., 2017; Chaudhry et al., 2018; Ritter et al., 2018; Serra et al., 2018; Dhar et al., 2019; Chaudhry et al., 2019; Lopez-Paz and Ranzato, 2017), 2) network expansion techniques for adding new parameters to a network to learn new information (Rusu et al., 2016; Yoon et al., 2018; Ostapenko et al., 2019; Hou et al., 2018), and 3) replay mechanisms for storing a representation of previous data to mix with new data when updating the network. Replay (or rehearsal) mechanisms have been shown to be the most effective of these approaches and are inspired by how the mammalian brain learns new information over time.

3.1 Replay in Supervised Learning

The ability of agents to learn over time from non-stationary data distributions without catastrophic forgetting is known as continual learning. Within continual learning, there are two major paradigms in which agents are trained (Parisi et al., 2019). The first paradigm, known as incremental batch learning, is the most common (Castro et al., 2018; Chaudhry et al., 2018; Fernando et al., 2017; Hou et al., 2019; Kemker and Kanan, 2018; Kemker et al., 2018; Rebuffi et al., 2017; Wu et al., 2019a; Zenke et al., 2017). In incremental batch learning, an agent is required to learn from a labelled dataset \mathcal{D} that is broken into T distinct *batches*. That is, $\mathcal{D} = \bigcup_{t=1}^T B_t$, where each B_t is a batch of data consisting of N_t labelled training samples, i.e., $B_t = \{(\mathbf{x}_i, \mathbf{y}_i)\}_{i=1}^{N_t}$ with $(\mathbf{x}_i, \mathbf{y}_i)$ denoting a training sample. At time t , the agent is required to learn from batch B_t by looping over the batch several times and making updates, before inference can be performed.

Although the incremental batch learning paradigm is popular in recent literature, it comes with caveats. Learning from batches is not biologically plausible and it is slow, which is not ideal for immediate learning. More specifically, mammals engage in resource constrained online learning from temporally correlated data streams, which is known as single pass online learning or *streaming learning*. Streaming learning is a special case of incremental batch learning where the batch size is set to one ($N_t = 1$) and the agent is only allowed a single epoch through the labelled training dataset (Gama, 2010; Gama et al., 2013). This paradigm closely resembles how humans and animals immediately learn from real-time data streams and can use new knowledge immediately.

Replay is one of the earliest (Hetherington, 1989) and most effective mechanisms for overcoming forgetting in both the incremental batch (Castro et al., 2018; Rebuffi et al., 2017; Wu et al., 2019a; Hou et al., 2019; Kemker and Kanan, 2018; Kemker et al., 2018) and streaming (Hayes et al., 2019, 2020; Chaudhry et al., 2019; Lopez-Paz and Ranzato, 2017) paradigms. There are two ways in which replay has been used in artificial neural networks: partial replay and generative replay (pseudo-rehearsal). For partial replay, an agent will store either all or a subset of previously learned inputs in a replay buffer. It then mixes either all, or a subset of, these previous inputs with new

samples and fine-tunes the network on this mixture. For example, several of the most successful models for incremental learning store a subset of previously learned raw inputs in a replay buffer (Gepperth and Karaoguz, 2016; Rebuffi et al., 2017; Lopez-Paz and Ranzato, 2017; Castro et al., 2018; Chaudhry et al., 2018; Nguyen et al., 2018; Hou et al., 2018; Hayes et al., 2019; Hou et al., 2019; Wu et al., 2019a; Lee et al., 2019; Belouadah and Popescu, 2019; Chaudhry et al., 2019; Riemer et al., 2019; Aljundi et al., 2019a,b; Belouadah and Popescu, 2020; He et al., 2020; Zhao et al., 2020; Kurlle et al., 2020; Chrysakis and Moens, 2020; Kim et al., 2020; Tao et al., 2020; Douillard et al., 2020). However, replaying raw pixels is not biologically plausible. More recently, methods that store representations/features from the middle (latent) layers of a network for replay have been developed (Hayes et al., 2020; Iscen et al., 2020; Caccia et al., 2019; Pellegrini et al., 2019), which are more consistent with replay in the mammalian brain, as suggested by hippocampal indexing theory (Teyler and Rudy, 2007) (see Sec. 2). The challenge in using representational replay comes in choosing which hidden layer(s) to use replay features from. While choosing features from earlier layers in the network allows more of the network to be trained incrementally, early features usually have larger spatial dimensions and require more memory for storage. Choosing the ideal layer for representational replay remains an open question.

In contrast to storing previous examples explicitly, generative replay methods train a generative model such as an auto-encoder or a generative adversarial network (GAN) (Goodfellow et al., 2014) to generate samples from previously learned data (Draelos et al., 2017; Kemker and Kanan, 2018; Robins, 1995; Ostapenko et al., 2019; Shin et al., 2017; He et al., 2018; French, 1997). Similar to partial replay methods, generative replay methods can generate veridical inputs (Shin et al., 2017; Kemker and Kanan, 2018; Parisi et al., 2018; He et al., 2018; Wu et al., 2018; Ostapenko et al., 2019; Abati et al., 2020; Liu et al., 2020b; Titsias et al., 2020; von Oswald et al., 2020; Ye and Bors, 2020) or mid-level CNN feature representations (van de Ven et al., 2020; Lao et al., 2020). These generative approaches do not require the explicit storage of data samples, which could potentially reduce storage requirements and mitigate some concerns regarding privacy. However, the generator itself often contains as many parameters as the classification network, leading to large memory requirements. Additionally, generative

Raw Replay Methods				Generative Replay Methods	
GeppNet	iCaRL	GEM	End-to-End	DGR	FearNet
RWALK	VCL	AD	ExStream	GDM	ESGR
LUCIR	BiC	GD	IL2M	MeRGAN	DGM
A-GEM	MER	MIR	REMIND	CCG	Mnemonics
GSS	ScaIL	ILOS	FA	FRCL	HNET
WA	GRS	CBRS	AQM	L-VAEGAN	
PRS	TPCIL	PODNet	ARI*	BI-R	DAFR

Figure 3: Categorizations of supervised artificial replay algorithms: Veridical Replay; Representational Replay; Generative Veridical Replay; Generative Representational Replay. See Appendix (Table 2) for algorithm citations.

models are notoriously difficult to train due to convergence issues and mode collapse, making these models less ideal for online learning. One advantage to using an unsupervised generative replay method is that the system could potentially be less susceptible to, but not completely unaffected by, catastrophic forgetting (Gillies, 1991). Additionally, generative replay is more biologically plausible as it is unrealistic to assume the human brain could store previous inputs explicitly, as is the case in partial replay. An overview of existing supervised replay methods for classification and their associated categorizations are in Fig. 3.

In addition to the aforementioned models that perform replay by storing a subset of previous inputs, there have been several models that use replay in conjunction with other mechanisms to mitigate forgetting, such as regularizing parameter updates. For example, the Gradient Episodic Memory (GEM) (Lopez-Paz and Ranzato, 2017) and Averaged-GEM (Chaudhry et al., 2019) models store a subset of previous inputs to use with a gradient regularization loss. Similarly, the Meta-Experience Replay model (Riemer et al., 2019) and Variational Continual Learning model (Nguyen et al., 2018) use experience replay in conjunction with meta-learning and Bayesian regularization techniques, respectively.

For both partial replay and generative replay approaches, the agent must decide *what* to replay. In (Chaudhry et al., 2018), four selection strategies are compared for storing

a small set of previous exemplars to use with a regularization approach. Namely, they compare uniform random sampling, storing examples closest to class decision boundaries, storing examples with the highest entropy, and storing a mean vector for each class in deep feature space. While they found storing a representative mean vector for each class performed the best, uniform random sampling performed nearly as well with less compute. In (Aljundi et al., 2019a), samples that would be the most interfered with after network updates are replayed to the network, i.e., those samples for which performance would be harmed the most by parameter updates. In their experiments, the authors found that replaying these interfered samples improved performance over randomly replaying samples. Similarly, in (Aljundi et al., 2019b) sample selection is formulated as a constrained optimization problem, which maximizes the chosen sample diversity. The authors of (Aljundi et al., 2019b) further propose a greedy sampling policy as an alternative to the optimization and find that both sample selection policies improve performance over random selection. Similarity scores have also been used to select replay samples (McClelland et al., 2020). While selective replay has demonstrated promising results in some small-scale settings, several large-scale studies have found that uniform random sampling works surprisingly well (Hayes et al., 2020; Wu et al., 2019a), achieving almost the same performance as more complicated techniques, while requiring less compute. The sample selection problem is also closely related to active learning strategies (Cohn et al., 1994; Lin and Parikh, 2017; Wang et al., 2016; Settles, 2009; Yoo and So Kweon, 2019; Wei et al., 2015), with the most common selection methods using uncertainty sampling (Lewis and Gale, 1994; Culotta and McCallum, 2005; Scheffer et al., 2001; Dagan and Engelson, 1995; Dasgupta and Hsu, 2008).

In addition to improving accuracy, selective replay can also facilitate better sample efficiency, i.e., the network requires fewer samples to learn new information. Sample efficiency has been studied for continual learning (Davidson and Mozer, 2020). In (Davidson and Mozer, 2020), the authors found that a convolutional neural network required fewer training epochs to reach a target accuracy on a new task after having learned other visually similar tasks. These findings are closely related to the multi-task learning literature, where the relationship between task similarity and network perfor-

mance in terms of accuracy and time has been studied (Zhang and Yang, 2017; Ruder, 2017; Standley et al., 2020; Liu et al., 2019a; Kendall et al., 2018).

While the majority of supervised learning literature has focused on overcoming forgetting in feed-forward or convolutional neural networks, there has also been work focused on using replay to mitigate forgetting in recurrent neural networks (Parisi et al., 2018; Sodhani et al., 2020). In (Parisi et al., 2018), a self-organizing recurrent network architecture consisting of a semantic memory and an episodic memory is introduced to replay previous neural reactivations. In (Sodhani et al., 2020), a network expansion technique is combined with gradient regularization and replay in a recurrent neural network to mitigate forgetting.

Further, in (Hayes et al., 2020; Greco et al., 2019), replay is used as an effective mechanism to mitigate forgetting for the problem of visual question answering, where an agent must answer natural language questions about images. Similarly, replay has been used for continual language learning (de Masson d’Autume et al., 2019). Replay has also been used to perform continual semantic segmentation of medical images (Ozdemir et al., 2018; Ozdemir and Goksel, 2019), remote sensing data (Tasar et al., 2019; Wu et al., 2019b), and on standard computer vision benchmarks (Cermelli et al., 2020). In (Acharya et al., 2020; Liu et al., 2020a), replay is used to mitigate forgetting for an continual object detection approach. Replay approaches have also been explored in continual learning for robotics (Lesort et al., 2020; Feng et al., 2019).

3.2 Replay in Reinforcement Learning

Experience replay has also been widely used in reinforcement learning (Mnih et al., 2015, 2013; Van Hasselt et al., 2016; Lillicrap et al., 2016; Lin, 1992; Adam et al., 2011; Foerster et al., 2017; Kapturowski et al., 2019). As in supervised classification, experience replay in reinforcement learning is inspired by the interplay between memory systems in the mammalian brain and its biological plausibility has been discussed in (Schaul et al., 2016; Hassabis et al., 2017). The overall goal of reinforcement learning is to train an agent to appropriately take actions in an environment to maximize its reward, which is a naturally realistic setup as compared to existing supervised

classification setups. In online reinforcement learning, an agent is required to learn from a temporally correlated stream of experiences. However, the temporal correlation of the input stream is not independent and identically distributed and violates the assumptions of conventional, gradient-based optimization algorithms typically used for updating agents, resulting in catastrophic forgetting. Lin (1992) proposed experience replay as a method for creating independent and identically distributed batches of data for an agent to learn from, while additionally allowing the agent to store and replay experiences that are rarely encountered. Specifically, the Deep Q-Network (DQN) (Mnih et al., 2013, 2015) performed experience replay using a sliding window approach where a uniformly selected set of previous transitions was replayed to the agent. While the random experience selection policy helped stabilize training of the DQN, prioritized experience replay (Schaul et al., 2016) has been shown to be more effective and efficient. Prioritized experience replay is based on the assumption that some transitions between experiences may be more surprising to the agent and additionally that some experiences might not be immediately relevant to an agent and should be replayed at a later point during training (Schmidhuber, 1991).

In (Schaul et al., 2016), prioritized experience replay was performed based on the magnitude of an experience’s temporal-difference (TD) error, which measures an agent’s learning progress and is consistent with biological findings (Singer and Frank, 2009; McNamara et al., 2014). However, using TD error alone can result in less diverse samples being replayed and must be combined with an importance-based sampling procedure. In (Isele and Cosgun, 2018), the authors compared four experience selection strategies to augment a first-in first-out queue, namely: TD error, absolute reward, distribution matching based on reservoir sampling, and state-space coverage maximization based on the nearest neighbors to an experience. They found that experience selection based on TD error and absolute reward did not work well in mitigating forgetting, while selection based on distribution matching and state-space coverage had comparable performance to an unlimited replay buffer. Although replay selection strategies have not shown as much benefit for the supervised learning scenario, they have significantly improved the performance and efficiency of training in reinforcement learning agents (Moore and Atkeson, 1993).

In standard prioritized experience replay, each experience is typically associated with a single goal (reward). In contrast, hindsight experience replay (Andrychowicz et al., 2017) allows experiences to be replayed with various rewards, which has several advantages. First, it allows learning when reward signals are sparse or binary, which is a common challenge in reinforcement learning agents. Overcoming sparse reward signals leads to sample efficiency. More interestingly, hindsight experience replay can serve as a form of curriculum learning (Bengio et al., 2009) by structuring the rewards such that they start off simple and grow increasingly more complex during training. Curriculum learning has been shown to speed up the training of neural networks, while also leading to better generalization (Bengio et al., 2009; Graves et al., 2017; Hunziker et al., 2018; Zhou and Bilmes, 2018; Fan et al., 2018; Achille et al., 2018). Additionally, curriculum learning is important for cognitive development in humans (Lenneberg, 1967; Senghas et al., 2004).

In addition to experience replay alone, several methods have also incorporated other brain-inspired mechanisms into their online reinforcement learning agents. For example, (Pritzel et al., 2017; Lengyel and Dayan, 2008; Blundell et al., 2016) take inspiration from the role the hippocampus plays in making decisions to develop agents that learn much faster than other approaches. In (Chen et al., 2019), the authors propose using only the raw environment pixel inputs for their agent in a trial-and-error scenario, which closely resembles how humans learn about and navigate their environments. In (Lake et al., 2017), it is argued that human brains are similar to model-free reinforcement learning agents for discrimination and associative learning tasks.

3.3 Replay in Unsupervised Learning

Although replay has been more extensively explored in supervised classification and reinforcement learning, it has also been explored in unsupervised learning settings (Lesort et al., 2019; Wu et al., 2018). For example, replay has been explored in continual learning of GANs for image and scene generation. Specifically, the Exemplar-Supported Generative Reproduction model (He et al., 2018) uses a GAN to generate pseudo-examples for replay during continual learning, while the Dynamic Generative Mem-

ory model (Ostapenko et al., 2019), the Deep Generative Replay model (Shin et al., 2017), the Memory Replay GAN model (Wu et al., 2018), and the Closed-Loop GAN model (Rios and Itti, 2018) are all used to continually learn to generate images and scenes. Continual learning with replay in GANs has also been used for reinforcement learning (Caselles-Dupré et al., 2019). Moreover, unsupervised learning techniques such as auto-encoders and GANs are widely used to generate replay samples in supervised learning algorithms (Draelos et al., 2017; Kemker and Kanan, 2018).

4 Juxtaposing Biological and Artificial Replay

Recently, machine learning researchers have tried to bridge some of the differences between biological replay and artificial replay. For example, several methods using representational replay (Hayes et al., 2020; Caccia et al., 2019; Pellegrini et al., 2019; Iscen et al., 2020) or generative representational replay (van de Ven et al., 2020; Lao et al., 2020), instead of veridical (raw pixel) replay, have been proposed to improve continual learning performance. Moreover, (McClelland et al., 2020) uses similarity scores in selecting which samples to replay based on evidence of replay in the hippocampus and cortex. Further, (Tadros et al., 2020b,a; Krishnan et al., 2019) implement a sleep-inspired mechanism in a converted spiking neural network to reduce catastrophic forgetting. More recently, (van de Ven et al., 2020) incorporated several brain-inspired mechanisms into their artificial network including feedback connections, context gating mechanisms, and generative representational replay.

However, many replay algorithms still differ from how humans learn and assimilate new information. For example, few existing techniques use Hebbian or error-based learning (Tao et al., 2020; Parisi et al., 2018) and most rely on supervised labels during training. Moreover, epigenetic tagging mechanisms in medial prefrontal cortex have largely been ignored by existing artificial network approaches and some approaches largely focus on replay during waking hours instead of replay during sleep (Hayes et al., 2019, 2020). In biological networks, replay happens both independently and concurrently in several different brain regions, whereas artificial replay implementations only perform replay at a single layer within the neural network. Furthermore, many exist-

ing artificial replay implementations 1) do not purge their memory buffer, which is not consistent with biology (Nádasdy et al., 1999; Karlsson and Frank, 2009) and 2) do not have a notion of waking (streaming/online) learning.

While selective experience replay has yielded significant performance gains in reinforcement learning, uniform random sampling still works well and is widely used in supervised classification, which is not consistent with how memories are selectively replayed in the brain. It is biologically infeasible to store everything a mammal encounters in its lifetime and likewise, it is not ideal for machine learning agents to store all previous data. In the case of partial replay, several different strategies have been explored for prioritizing what memories should be replayed (Chaudhry et al., 2018; Aljundi et al., 2019b,a; McClelland et al., 2020). While there have been several replay selection methods proposed, many existing works have found uniform random sampling of previous memories to work well, especially for large-scale problems (Chaudhry et al., 2018; Wu et al., 2019a; Hayes et al., 2020). While sampling strategies have not demonstrated significant success for supervised learning problems, the reinforcement learning community has seen more benefit from these approaches, e.g., prioritized experience replay (Schaul et al., 2016) and hindsight replay (Andrychowicz et al., 2017). Exploring selective replay strategies in machine learning could help inform biologists about what might be replayed in the brain. Further, the efficiency of selective replay in machine learning has largely been ignored with most researchers developing selective replay methods that only yield better performance. By studying selective replay techniques that are efficient, the agent could potentially learn information better and more quickly, which is closely related to forward knowledge transfer in humans. Moreover, humans generate novel memories that are not generated from external world inputs during REM sleep (Lewis et al., 2018). Exploring schemes to generate novel memories in machine learning could further improve performance.

In machine learning and computer vision, there have been several models inspired by CLS theory in biological networks (Gepperth and Karaoguz, 2016; French, 1997; Ans and Rousset, 1997; Kemker and Kanan, 2018; Robins, 1995). All of these models have a fast-learning hippocampal-inspired network and consolidate knowledge to a medial prefrontal cortex network that learns more slowly. Further, (Gepperth and

Karaoguz, 2016; Kemker and Kanan, 2018; Draelos et al., 2017) integrate neurogenesis into their models where new neurons are created to form new memories. Several of these CLS-inspired models focus on using generative replay to generate new inputs during training (French, 1997; Ans and Rousset, 1997; Kemker and Kanan, 2018; Robins, 1995), instead of storing raw inputs explicitly (Gepperth and Karaoguz, 2016). However, the vast majority of existing replay approaches in artificial neural networks replay raw pixel inputs (Hou et al., 2019; Rebuffi et al., 2017; Castro et al., 2018; Wu et al., 2019a). There have been a few approaches that store high-level feature representations (feature maps) of inputs instead of using generative replay (Hayes et al., 2019, 2020; Pellegrini et al., 2019; Caccia et al., 2019), which is more biologically plausible than replay from raw pixels. While there have been several models inspired by CLS theory (Gepperth and Karaoguz, 2016; French, 1997; Ans and Rousset, 1997; Kemker and Kanan, 2018; Robins, 1995), many existing replay approaches have only focused on modeling medial prefrontal cortex directly and do not have a fast learning network. Moreover, (Kemker and Kanan, 2018) is the only CLS-inspired model that integrates a non-oracle basolateral amygdala network for decision-making during inference. Lastly, none of the aforementioned CLS-inspired models use information from the neocortex-inspired network to influence training of the hippocampal-inspired network, whereas the neocortex influences learning in the hippocampus and vice-versa in biological networks.

Further, CLS theory assumes that different awake and sleep states correspond to periods of encoding memories in hippocampus and the subsequent transfer of memories from hippocampus to cortex. This suggests that artificial neural networks could benefit from the inclusion of explicit awake and sleep states, inspired by the mammalian brain. Moreover, one open question in biology involves what happens to memories after they have been consolidated from the hippocampus to the neocortex. These memories in hippocampus could be erased entirely, or they could still be encoded in the hippocampus, but never reactivated again. While this is an open question in biology, its exploration in machine learning could inform the neuroscientific community and lead to new discoveries.

While the CLS memory model (i.e., fast learning in hippocampus followed by slow

learning in the cortex) is widely accepted as a core principle of how the brain learns declarative memories, it is likely not the only memory model the brain uses. Indeed, procedural, presumably hippocampus-independent memories, e.g., some motor tasks (Fogel and Smith, 2006) can be learned without forgetting old skills and replayed during REM sleep when the hippocampus is effectively disconnected from the neocortex. Even if the hippocampus may be important for early phases of motor learning, subsequent training and replay rely on motor cortex and striatal networks (Lemke et al., 2019). Therefore, while typical machine learning replay approaches interleave new training data with old knowledge from hippocampus-like networks, the biological cortex is capable of replaying old traces on its own. For example, very few researchers have explored “self-generated” replay as a mechanism to protect old knowledge for continual learning (Tadros et al., 2020b,a; Krishnan et al., 2019).

Another critical difference between biological and artificial implementations of replay is the notion of regularization. In biological networks, normalization and synaptic changes co-occur with replay (Chauvette et al., 2012; Tononi and Cirelli, 2014). However, in artificial networks, regularization and replay approaches for mitigating catastrophic forgetting have largely been explored independently. While some deep learning methods combine replay and regularization (Chaudhry et al., 2019; Lopez-Paz and Ranzato, 2017), each mechanism operates largely without informed knowledge of the other, unlike the co-occurrence and direct communication between the two mechanisms in biology. By integrating the two mechanisms with more communication in artificial networks, performance could be improved further and each mechanism could potentially strengthen the other component. For example, replay informed regularization could help strengthen connections specific to a particular memory, while regularization informed replay could help identify which samples to replay that will enable more transfer or less forgetting.

5 Conclusions

Although humans and animals are able to continuously acquire new information over their lifetimes without catastrophically forgetting prior knowledge, artificial neural net-

works lack these capabilities (Parisi et al., 2019; Kemker et al., 2018; De Lange et al., 2019). Replay of previous experiences or memories in humans has been identified as the primary mechanism for overcoming forgetting and enabling continual knowledge acquisition (Walker and Stickgold, 2004). While replay-inspired mechanisms have enabled artificial networks to learn from non-stationary data distributions, these mechanisms differ from biological replay in several ways. Moreover, current artificial replay implementations are computationally expensive to deploy. In this paper, we have given an overview of the current state of research in both artificial and biological implementations of replay and further identified several gaps between the two fields. By incorporating more biological mechanisms into artificial replay implementations, we hope deep networks will exhibit better transfer, abstraction, and generalization. Further, we hope that advancing replay in artificial networks can inform future neuroscientific studies of replay in biology.

Acknowledgments

TH and CK were supported in part by the DARPA/SRI Lifelong Learning Machines program [HR0011-18-C-0051], AFOSR grant [FA9550-18-1-0121], and NSF award #1909696. MB and GK were supported in part by the Lifelong Learning Machines program from DARPA/MTO [HR0011-18-2-0021], ONR grant [N000141310672], NSF award [IIS-1724405], and NIH grant [R01MH125557]. The views and conclusions contained herein are those of the authors and should not be interpreted as representing the official policies or endorsements of any sponsor. One author in this study, CK, was employed at a commercial company, Paige, New York during the preparation of this manuscript. This company played no role in the sponsorship, design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix

Table 2: Replay algorithm citations from Fig. 3.

ALGORITHM	CITATION
<i>Veridical Replay</i>	
GeppNet	(Gepperth and Karaoguz, 2016)
iCaRL	(Rebuffi et al., 2017)
GEM	(Lopez-Paz and Ranzato, 2017)
End-to-End	(Castro et al., 2018)
RWALK	(Chaudhry et al., 2018)
VCL	(Nguyen et al., 2018)
AD	(Hou et al., 2018)
ExStream	(Hayes et al., 2019)
LUCIR	(Hou et al., 2019)
BiC	(Wu et al., 2019a)
GD	(Lee et al., 2019)
IL2M	(Belouadah and Popescu, 2019)
A-GEM	(Chaudhry et al., 2019)
MER	(Riemer et al., 2019)
MIR	(Aljundi et al., 2019a)
GSS	(Aljundi et al., 2019b)
ScaIL	(Belouadah and Popescu, 2020)
ILOS	(He et al., 2020)
WA	(Zhao et al., 2020)
GRS	(Kurle et al., 2020)
CBRS	(Chrysakis and Moens, 2020)
PRS	(Kim et al., 2020)
TPCIL	(Tao et al., 2020)
PODNet	(Douillard et al., 2020)
<i>Representational Replay</i>	
REMIND	(Hayes et al., 2020)

Continued on next page

Table 2 – *Continued from previous page*

ALGORITHM	CITATION
FA	(Isken et al., 2020)
AQM	(Caccia et al., 2019)
AR1*	(Pellegrini et al., 2019)
<i>Generative Veridical Replay</i>	
DGR	(Shin et al., 2017)
FearNet	(Kemker and Kanan, 2018)
GDM	(Parisi et al., 2018)
ESGR	(He et al., 2018)
MeRGAN	(Wu et al., 2018)
DGM	(Ostapenko et al., 2019)
CCG	(Abati et al., 2020)
Mnemonics	(Liu et al., 2020b)
FRCL	(Titsias et al., 2020)
HNET	(von Oswald et al., 2020)
L-VAEGAN	(Ye and Bors, 2020)
<i>Generative Representational Replay</i>	
BI-R	(van de Ven et al., 2020)
DAFR	(Lao et al., 2020)

References

- Abati, D., Tomczak, J., Blankevoort, T., Calderara, S., Cucchiara, R., and Bejnordi, B. E. (2020). Conditional channel gated networks for task-aware continual learning. In *CVPR*, pages 3931–3940.
- Abbott, L. F. and Nelson, S. B. (2000). Synaptic plasticity: taming the beast. *Nature neuroscience*, 3(11):1178–1183.

- Abraham, W. C. and Robins, A. (2005). Memory retention – the synaptic stability versus plasticity dilemma. *Trends in Neurosciences*, 28(2):73–78.
- Acharya, M., Hayes, T. L., and Kanan, C. (2020). Rodeo: Replay for online object detection. In *BMVC*.
- Achille, A., Rovere, M., and Soatto, S. (2018). Critical learning periods in deep networks. In *ICLR*.
- Adam, S., Busoniu, L., and Babuska, R. (2011). Experience replay for real-time reinforcement learning control. *IEEE Transactions on Systems, Man, and Cybernetics, Part C (Applications and Reviews)*, 42(2):201–212.
- Albouy, G., Fogel, S., Pottiez, H., Nguyen, V. A., Ray, L., Lungu, O., Carrier, J., Robertson, E., and Doyon, J. (2013). Daytime sleep enhances consolidation of the spatial but not motoric representation of motor sequence memory. *PloS one*, 8(1):e52805.
- Aljundi, R., Babiloni, F., Elhoseiny, M., Rohrbach, M., and Tuytelaars, T. (2018). Memory aware synapses: Learning what (not) to forget. In *ECCV*, pages 139–154.
- Aljundi, R., Belilovsky, E., Tuytelaars, T., Charlin, L., Caccia, M., Lin, M., and Page-Caccia, L. (2019a). Online continual learning with maximal interfered retrieval. In *NeurIPS*, pages 11849–11860.
- Aljundi, R., Lin, M., Goujaud, B., and Bengio, Y. (2019b). Gradient based sample selection for online continual learning. In *NeurIPS*, pages 11816–11825.
- Ambrose, R. E., Pfeiffer, B. E., and Foster, D. J. (2016). Reverse Replay of Hippocampal Place Cells Is Uniquely Modulated by Changing Reward. *Neuron*, 91(5):1124–1136.
- Andrychowicz, M., Wolski, F., Ray, A., Schneider, J., Fong, R., Welinder, P., McGrew, B., Tobin, J., Abbeel, O. P., and Zaremba, W. (2017). Hindsight experience replay. In *Advances in neural information processing systems*, pages 5048–5058.

- Ans, B. and Rousset, S. (1997). Avoiding catastrophic forgetting by coupling two reverberating neural networks. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*, 320(12):989–997.
- Bader, R., Mecklinger, A., Hoppstädter, M., and Meyer, P. (2010). Recognition memory for one-trial-unitized word pairs: Evidence from event-related potentials. *NeuroImage*, 50(2):772–781.
- Baird, B., Smallwood, J., Mrazek, M. D., Kam, J. W., Franklin, M. S., and Schooler, J. W. (2012). Inspired by distraction: Mind wandering facilitates creative incubation. *Psychological science*, 23(10):1117–1122.
- Barakat, M., Carrier, J., Debas, K., Lungu, O., Fogel, S., Vandewalle, G., Hoge, R. D., Bellec, P., Karni, A., and Ungerleider, L. G. (2013). Sleep spindles predict neural and behavioral changes in motor sequence consolidation. *Human brain mapping*, 34(11):2918–2928.
- Baran, B., Pace-Schott, E. F., Ericson, C., and Spencer, R. M. C. (2012). Processing of Emotional Reactivity and Emotional Memory over Sleep. *Journal of Neuroscience*, 32(3):1035–1042.
- Battaglia, F. P., Sutherland, G. R., and McNaughton, B. L. (2004). Hippocampal sharp wave bursts coincide with neocortical “up-state” transitions. *Learning & memory*, 11(6):697–704.
- Bazhenov, M. and Timofeev, I. (2006). Thalamocortical oscillations. *Scholarpedia*, 1(6):1319.
- Belouadah, E. and Popescu, A. (2019). Il2m: Class incremental learning with dual memory. In *ICCV*, pages 583–592.
- Belouadah, E. and Popescu, A. (2020). Scail: Classifier weights scaling for class incremental learning. In *WACV*, pages 1266–1275.
- Belouadah, E., Popescu, A., and Kanellos, I. (2020). A comprehensive study of class incremental learning algorithms for visual tasks. *Neural Networks*.

- Bengio, Y., Louradour, J., Collobert, R., and Weston, J. (2009). Curriculum Learning. In *ICML*, pages 41–48.
- Bero, A. W., Meng, J., Cho, S., Shen, A. H., Canter, R. G., Ericsson, M., and Tsai, L.-H. (2014). Early remodeling of the neocortex upon episodic memory encoding. *Proceedings of the National Academy of Sciences*, 111(32):11852–11857.
- Bi, G.-q. and Poo, M.-m. (1998). Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *Journal of neuroscience*, 18(24):10464–10472.
- Blundell, C., Uria, B., Pritzel, A., Li, Y., Ruderman, A., Leibo, J. Z., Rae, J., Wierstra, D., and Hassabis, D. (2016). Model-free episodic control. *arXiv preprint arXiv:1606.04460*.
- Bontempi, B., Laurent-Demir, C., Destrade, C., and Jaffard, R. (1999). Time-dependent reorganization of brain circuitry underlying long-term memory storage. *Nature*, 400(6745):671–675.
- Born, J. (2010). Slow-Wave Sleep and the Consolidation of Long-Term Memory. *The World Journal of Biological Psychiatry*, 11(sup1):16–21.
- Brown, R. E., Basheer, R., McKenna, J. T., Strecker, R. E., and McCarley, R. W. (2012). Control of Sleep and Wakefulness. *Physiological reviews*, 92(3):1087–1187.
- Brown, R. M. and Robertson, E. M. (2007). Off-Line Processing: Reciprocal Interactions between Declarative and Procedural Memories. *Journal of Neuroscience*, 27(39):10468–10475.
- Buzsáki, G. (2015). Hippocampal sharp wave-ripple: A cognitive biomarker for episodic memory and planning. *Hippocampus*, 25(10):1073–1188.
- Buzsaki, G., Horvath, Z., Urioste, R., Hetke, J., and Wise, K. (1992). High-frequency network oscillation in the hippocampus. *Science*, 256(5059):1025–1027.
- Caccia, L., Belilovsky, E., Caccia, M., and Pineau, J. (2019). Online learned continual compression with adaptive quantization modules. *arXiv*, pages arXiv–1911.

- Cai, D. J., Mednick, S. A., Harrison, E. M., Kanady, J. C., and Mednick, S. C. (2009). Rem, not incubation, improves creativity by priming associative networks. *Proceedings of the National Academy of Sciences*, 106(25):10130–10134.
- Caselles-Dupré, H., Garcia-Ortiz, M., and Filliat, D. (2019). S-trigger: Continual state representation learning via self-triggered generative replay. *arXiv preprint arXiv:1902.09434*.
- Castro, F. M., Marín-Jiménez, M. J., Guil, N., Schmid, C., and Alahari, K. (2018). End-to-end incremental learning. In *ECCV*, pages 233–248.
- Cazé, R., Khamassi, M., Aubin, L., and Girard, B. (2018). Hippocampal replays under the scrutiny of reinforcement learning models. *Journal of Neurophysiology*, 120(6):2877–2896.
- Cermelli, F., Mancini, M., Bulò, S. R., Ricci, E., and Caputo, B. (2020). Modeling the background for incremental learning in semantic segmentation. In *CVPR*, pages 9233–9242.
- Chaudhry, A., Dokania, P. K., Ajanthan, T., and Torr, P. H. (2018). Riemannian walk for incremental learning: Understanding forgetting and intransigence. In *ECCV*, pages 532–547.
- Chaudhry, A., Ranzato, M., Rohrbach, M., and Elhoseiny, M. (2019). Efficient lifelong learning with A-GEM. In *ICLR*.
- Chauvette, S., Seigneur, J., and Timofeev, I. (2012). Sleep oscillations in the thalamo-cortical system induce long-term neuronal plasticity. *Neuron*, 75(6):1105–1113.
- Chen, J., Chen, J., Zhang, R., and Hu, X. (2019). Toward a brain-inspired system: Deep recurrent reinforcement learning for a simulated self-driving agent. *Frontiers in neurorobotics*, 13.
- Chrysakis, A. and Moens, M.-F. (2020). Online continual learning from imbalanced data. *Proceedings of Machine Learning and Systems*, pages 8303–8312.

- Cohen, D. A., Pascual-Leone, A., Press, D. Z., and Robertson, E. M. (2005). Off-line learning of motor skill memory: A double dissociation of goal and movement. *Proceedings of the National Academy of Sciences*, 102(50):18237–18241.
- Cohn, D., Atlas, L., and Ladner, R. (1994). Improving generalization with active learning. *Machine learning*, 15(2):201–221.
- Culotta, A. and McCallum, A. (2005). Reducing labeling effort for structured prediction tasks. In *AAAI*, volume 5, pages 746–751.
- Dagan, I. and Engelson, S. P. (1995). Committee-based sampling for training probabilistic classifiers. In *Machine Learning Proceedings 1995*, pages 150–157. Elsevier.
- Dasgupta, S. and Hsu, D. (2008). Hierarchical sampling for active learning. In *ICML*, pages 208–215. ACM.
- Davidson, G. and Mozer, M. C. (2020). Sequential mastery of multiple visual tasks: Networks naturally learn to learn and forget to forget. In *CVPR*, pages 9282–9293.
- Davidson, T. J., Kloosterman, F., and Wilson, M. A. (2009). Hippocampal Replay of Extended Experience. *Neuron*, 63(4):497–507.
- De Lange, M., Aljundi, R., Masana, M., Parisot, S., Jia, X., Leonardis, A., Slabaugh, G., and Tuytelaars, T. (2019). A continual learning survey: Defying forgetting in classification tasks. *arXiv preprint arXiv:1909.08383*.
- de Masson d’Autume, C., Ruder, S., Kong, L., and Yogatama, D. (2019). Episodic memory in lifelong language learning. In *Advances in Neural Information Processing Systems*, pages 13122–13131.
- Debas, K., Carrier, J., Orban, P., Barakat, M., Lungu, O., Vandewalle, G., Tahar, A. H., Bellec, P., Karni, A., and Ungerleider, L. G. (2010). Brain plasticity related to the consolidation of motor sequence learning and motor adaptation. *Proceedings of the National Academy of Sciences*, 107(41):17839–17844.
- Dhar, P., Singh, R. V., Peng, K.-C., Wu, Z., and Chellappa, R. (2019). Learning without memorizing. In *CVPR*, pages 5138–5146.

- Diekelmann, S. (2014). Sleep for cognitive enhancement. *Frontiers in Systems Neuroscience*, 8.
- Djonlagic, I., Rosenfeld, A., Shohamy, D., Myers, C., Gluck, M., and Stickgold, R. (2009). Sleep enhances category learning. *Learning & memory*, 16(12):751–755.
- Douillard, A., Cord, M., Ollion, C., Robert, T., and Valle, E. (2020). Podnet: Pooled outputs distillation for small-tasks incremental learning. In *ECCV*, pages 86–102.
- Draelos, T. J., Miner, N. E., Lamb, C. C., Cox, J. A., Vineyard, C. M., Carlson, K. D., Severa, W. M., James, C. D., and Aimone, J. B. (2017). Neurogenesis deep learning: Extending deep networks to accommodate new classes. In *2017 International Joint Conference on Neural Networks (IJCNN)*, pages 526–533. IEEE.
- Dumay, N. and Gaskell, M. G. (2007). Sleep-associated changes in the mental representation of spoken words. *Psychological Science*, 18(1):35–39.
- Durrant, S. J., Cairney, S. A., McDermott, C., and Lewis, P. A. (2015). Schema-conformant memories are preferentially consolidated during rem sleep. *Neurobiology of Learning and Memory*, 122:41–50.
- Eckert, M., McNaughton, B., and Tatsuno, M. (2020). Neural ensemble reactivation in rapid eye movement and slow-wave sleep coordinate with muscle activity to promote rapid motor skill learning. *Philosophical Transactions of the Royal Society B*, 375(1799):20190655.
- Ellenbogen, J. M., Hu, P. T., Payne, J. D., Titone, D., and Walker, M. P. (2007). Human relational memory requires time and sleep. *Proceedings of the National Academy of Sciences*, 104(18):7723–7728.
- Euston, D. R., Tatsuno, M., and McNaughton, B. L. (2007). Fast-forward playback of recent memory sequences in prefrontal cortex during sleep. *science*, 318(5853):1147–1150.
- Fan, Y., Tian, F., Qin, T., Li, X.-Y., and Liu, T.-Y. (2018). Learning to teach. In *ICLR*.

- Feng, F., Chan, R. H., Shi, X., Zhang, Y., and She, Q. (2019). Challenges in task incremental learning for assistive robotics. *IEEE Access*.
- Fernando, C., Banarse, D., Blundell, C., Zwols, Y., Ha, D., Rusu, A. A., Pritzel, A., and Wierstra, D. (2017). Pathnet: Evolution channels gradient descent in super neural networks. *arXiv:1701.08734*.
- Foerster, J., Nardelli, N., Farquhar, G., Afouras, T., Torr, P. H., Kohli, P., and Whiteson, S. (2017). Stabilising experience replay for deep multi-agent reinforcement learning. In *ICML*, pages 1146–1155. JMLR. org.
- Fogel, S. M. and Smith, C. T. (2006). Learning-dependent changes in sleep spindles and stage 2 sleep. *Journal of sleep research*, 15(3):250–255.
- Foster, D. J. (2017). Replay comes of age. *Annual review of neuroscience*, 40:581–602.
- Foster, D. J. and Knierim, J. J. (2012). Sequence learning and the role of the hippocampus in rodent navigation. *Current Opinion in Neurobiology*, 22(2):294–300.
- Foster, D. J. and Wilson, M. A. (2006). Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature*, 440(7084):680–683.
- French, R. M. (1997). Pseudo-recurrent connectionist networks: An approach to the ‘sensitivity-stability’ dilemma. *Connection Science*, 9(4):353–380.
- French, R. M. (1999). Catastrophic forgetting in connectionist networks. *Trends in Cognitive Sciences*, 3(4):128–135.
- Gama, J. (2010). *Knowledge discovery from data streams*. Chapman and Hall/CRC.
- Gama, J., Sebastião, R., and Rodrigues, P. P. (2013). On evaluating stream learning algorithms. *Machine learning*, 90(3):317–346.
- Gepperth, A. and Karaoguz, C. (2016). A bio-inspired incremental learning architecture for applied perceptual problems. *Cognitive Computation*, 8(5):924–934.

- Gillies, A. (1991). *The Stability/Plasticity Dilemma in Self-organising Neural Networks*. PhD thesis, MSc Thesis, Computer Science Department, University of Otago, New Zealand.
- Golden, R., Delanois, J. E., Sanda, P., and Bazhenov, M. (2020). Sleep prevents catastrophic forgetting in spiking neural networks by forming joint synaptic weight representations. *bioRxiv*, page 688622.
- Gómez, R. L., Bootzin, R. R., and Nadel, L. (2006). Naps promote abstraction in language-learning infants. *Psychological science*, 17(8):670–674.
- González, O. C., Sokolov, Y., Krishnan, G. P., Delanois, J. E., and Bazhenov, M. (2020). Can sleep protect memories from catastrophic forgetting? *Elife*, 9:e51005.
- Goodfellow, I., Pouget-Abadie, J., Mirza, M., Xu, B., Warde-Farley, D., Ozair, S., Courville, A., and Bengio, Y. (2014). Generative adversarial nets. In *NeurIPS*, pages 2672–2680.
- Graves, A., Bellemare, M. G., Menick, J., Munos, R., and Kavukcuoglu, K. (2017). Automated curriculum learning for neural networks. In *ICML*, pages 1311–1320. JMLR.org.
- Greco, C., Plank, B., Fernández, R., and Bernardi, R. (2019). Psycholinguistics meets continual learning: Measuring catastrophic forgetting in visual question answering. In *Proceedings of the 57th Annual Meeting of the Association for Computational Linguistics*, pages 3601–3605, Florence, Italy. Association for Computational Linguistics.
- Grosmark, A. D., Mizuseki, K., Pastalkova, E., Diba, K., and Buzsáki, G. (2012). REM Sleep Reorganizes Hippocampal Excitability. *Neuron*, 75(6):1001–1007.
- Gulati, T., Guo, L., Ramanathan, D. S., Bodepudi, A., and Ganguly, K. (2017). Neural reactivations during sleep determine network credit assignment. *Nature*, 201:7.
- Gulati, T., Ramanathan, D. S., Wong, C. C., and Ganguly, K. (2014). Reactivation of

- emergent task-related ensembles during slow-wave sleep after neuroprosthetic learning. *Nature Neuroscience*, 17(8):1107.
- Gupta, A. S., van der Meer, M. A., Touretzky, D. S., and Redish, A. D. (2010). Hippocampal Replay Is Not a Simple Function of Experience. *Neuron*, 65(5):695–705.
- Haskins, A. L., Yonelinas, A. P., Quamme, J. R., and Ranganath, C. (2008). Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron*, 59(4):554–560.
- Hassabis, D., Kumaran, D., Summerfield, C., and Botvinick, M. (2017). Neuroscience-inspired artificial intelligence. *Neuron*, 95(2):245–258.
- Hayes, T. L., Cahill, N. D., and Kanan, C. (2019). Memory efficient experience replay for streaming learning. In *ICRA*, pages 9769–9776.
- Hayes, T. L., Kaffe, K., Shrestha, R., Acharya, M., and Kanan, C. (2020). Remind your neural network to prevent catastrophic forgetting. In *ECCV*, pages 466–483.
- He, C., Wang, R., Shan, S., and Chen, X. (2018). Exemplar-supported generative reproduction for class incremental learning. In *BMVC*, page 98.
- He, J., Mao, R., Shao, Z., and Zhu, F. (2020). Incremental learning in online scenario. In *CVPR*, pages 13926–13935.
- Hetherington, P. (1989). Is there ‘catastrophic interference’ in connectionist networks? In *Proceedings of the 11th annual conference of the cognitive science society*, pages 26–33. LEA.
- Hou, S., Pan, X., Change Loy, C., Wang, Z., and Lin, D. (2018). Lifelong learning via progressive distillation and retrospection. In *ECCV*, pages 437–452.
- Hou, S., Pan, X., Wang, Z., Change Loy, C., and Lin, D. (2019). Learning a unified classifier incrementally via rebalancing. In *CVPR*, pages 831–839.
- Hu, P., Stylos-Allan, M., and Walker, M. P. (2006). Sleep Facilitates Consolidation of Emotional Declarative Memory. *Psychological Science*, 17(10):891–898.

- Hunziker, A., Chen, Y., Mac Aodha, O., Rodriguez, M. G., Krause, A., Perona, P., Yue, Y., and Singla, A. (2018). Teaching multiple concepts to forgetful learners. *preprint arXiv:1805.08322*.
- Iscen, A., Zhang, J., Lazebnik, S., and Schmid, C. (2020). Memory-efficient incremental learning through feature adaptation. In *ECCV*, pages 699–715.
- Isele, D. and Cosgun, A. (2018). Selective experience replay for lifelong learning. In *AAAI*, pages 3302–3309.
- Ji, D. and Wilson, M. A. (2007a). Coordinated Memory Replay in the Visual Cortex and Hippocampus during Sleep. *Nat Neurosci*, 10(1):100–107.
- Ji, D. and Wilson, M. A. (2007b). Coordinated Memory Replay in the Visual Cortex and Hippocampus during Sleep. *Nat Neurosci*, 10(1):100–107.
- Johnson, A. and Redish, A. D. (2007). Neural ensembles in ca3 transiently encode paths forward of the animal at a decision point. *Journal of Neuroscience*, 27(45):12176–12189.
- Kapturowski, S., Ostrovski, G., Dabney, W., Quan, J., and Munos, R. (2019). Recurrent experience replay in distributed reinforcement learning. In *ICLR*.
- Karlsson, M. P. and Frank, L. M. (2009). Awake Replay of Remote Experiences in the Hippocampus. *Nature neuroscience*, 12(7):913–918.
- Kemker, R. and Kanan, C. (2018). FearNet: Brain-inspired model for incremental learning. In *ICLR*.
- Kemker, R., McClure, M., Abitino, A., Hayes, T. L., and Kanan, C. (2018). Measuring catastrophic forgetting in neural networks. In *AAAI*.
- Kendall, A., Gal, Y., and Cipolla, R. (2018). Multi-task learning using uncertainty to weigh losses for scene geometry and semantics. In *CVPR*, pages 7482–7491.
- Kim, C. D., Jeong, J., and Kim, G. (2020). Imbalanced continual learning with partitioning reservoir sampling. In *ECCV*, pages 411–428.

- King, B. R., Hoedlmoser, K., Hirschauer, F., Dolfen, N., and Albouy, G. (2017). Sleep-
ing on the motor engram: The multifaceted nature of sleep-related motor memory
consolidation. *Neuroscience & Biobehavioral Reviews*, 80:1–22.
- Kirkpatrick, J., Pascanu, R., Rabinowitz, N., Veness, J., Desjardins, G., Rusu, A. A.,
Milan, K., Quan, J., Ramalho, T., Grabska-Barwinska, A., Hassabis, D., Clopath, C.,
Kumaran, D., and Hadsell, R. (2017). Overcoming catastrophic forgetting in neural
networks. *PNAS*.
- Kitamura, T., Ogawa, S. K., Roy, D. S., Okuyama, T., Morrissey, M. D., Smith, L. M.,
Redondo, R. L., and Tonegawa, S. (2017). Engrams and circuits crucial for systems
consolidation of a memory. *Science*, 356(6333):73–78.
- Krishnan, G. P., Chauvette, S., Shamie, I., Soltani, S., Timofeev, I., Cash, S. S., Halgren,
E., and Bazhenov, M. (2016). Cellular and Neurochemical Basis of Sleep Stages in
the Thalamocortical Network. *eLife*, 5:e18607.
- Krishnan, G. P., Tadros, T., Ramyaa, R., and Bazhenov, M. (2019). Biolog-
ically inspired sleep algorithm for artificial neural networks. *arXiv preprint*
arXiv:1908.02240.
- Kudrimoti, H. S., Barnes, C. A., and McNaughton, B. L. (1999). Reactivation of Hip-
pocampal Cell Assemblies: Effects of Behavioral State, Experience, and EEG Dy-
namics. *The Journal of Neuroscience*, 19(10):4090–4101.
- Kumaran, D., Hassabis, D., and McClelland, J. L. (2016). What learning systems do
intelligent agents need? complementary learning systems theory updated. *Trends in*
cognitive sciences, 20(7):512–534.
- Kuriyama, K., Stickgold, R., and Walker, M. P. (2004). Sleep-dependent learning and
motor-skill complexity. *Learning & memory*, 11(6):705–713.
- Kurle, R., Cseke, B., Klushyn, A., van der Smagt, P., and Günnemann, S. (2020). Con-
tinual learning with bayesian neural networks for non-stationary data. In *ICLR*.

- Lake, B. M., Ullman, T. D., Tenenbaum, J. B., and Gershman, S. J. (2017). Building machines that learn and think like people. *Behavioral and brain sciences*, 40.
- Lao, Q., Jiang, X., Havaei, M., and Bengio, Y. (2020). Continuous domain adaptation with variational domain-agnostic feature replay. *arXiv preprint arXiv:2003.04382*.
- Lee, A. K. and Wilson, M. A. (2002). Memory of Sequential Experience in the Hippocampus during Slow Wave Sleep. *Neuron*, 36(6):1183–1194.
- Lee, K., Lee, K., Shin, J., and Lee, H. (2019). Overcoming catastrophic forgetting with unlabeled data in the wild. In *ICCV*, pages 312–321.
- Lemke, S. M., Ramanathan, D. S., Guo, L., Won, S. J., and Ganguly, K. (2019). Emergent modular neural control drives coordinated motor actions. *Nature neuroscience*, 22(7):1122–1131.
- Lengyel, M. and Dayan, P. (2008). Hippocampal contributions to control: the third way. In *Advances in neural information processing systems*, pages 889–896.
- Lenneberg, E. H. (1967). The biological foundations of language. *Hospital Practice*, 2(12):59–67.
- Lesburguères, E., Gobbo, O. L., Alaux-Cantin, S., Hambucken, A., Trifilieff, P., and Bontempi, B. (2011). Early tagging of cortical networks is required for the formation of enduring associative memory. *Science*, 331(6019):924–928.
- Lesort, T., Caselles-Dupré, H., Garcia-Ortiz, M., Stoian, A., and Filliat, D. (2019). Generative models from the perspective of continual learning. In *2019 International Joint Conference on Neural Networks (IJCNN)*, pages 1–8. IEEE.
- Lesort, T., Lomonaco, V., Stoian, A., Maltoni, D., Filliat, D., and Díaz-Rodríguez, N. (2020). Continual learning for robotics: Definition, framework, learning strategies, opportunities and challenges. *Information Fusion*, 58:52–68.
- Lewis, D. D. and Gale, W. A. (1994). A sequential algorithm for training text classifiers. In *SIGIR’94*, pages 3–12. Springer.

- Lewis, P. A. and Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends in Cognitive Sciences*, 15(8):343–351.
- Lewis, P. A., Knoblich, G., and Poe, G. (2018). How Memory Replay in Sleep Boosts Creative Problem-Solving. *Trends in Cognitive Sciences*, 22(6):491–503.
- Li, W., Ma, L., Yang, G., and Gan, W.-B. (2017). Rem sleep selectively prunes and maintains new synapses in development and learning. *Nature neuroscience*, 20(3):427–437.
- Lillicrap, T. P., Hunt, J. J., Pritzel, A., Heess, N., Erez, T., Tassa, Y., Silver, D., and Wierstra, D. (2016). Continuous control with deep reinforcement learning. In *ICLR*.
- Lin, L.-J. (1992). Self-improving reactive agents based on reinforcement learning, planning and teaching. *Machine Learning*, 8(3-4):293–321.
- Lin, X. and Parikh, D. (2017). Active learning for visual question answering: An empirical study. *arXiv:1711.01732*.
- Liu, S., Johns, E., and Davison, A. J. (2019a). End-to-end multi-task learning with attention. In *CVPR*, pages 1871–1880.
- Liu, X., Yang, H., Ravichandran, A., Bhotika, R., and Soatto, S. (2020a). Continual universal object detection. *arXiv preprint arXiv:2002.05347*.
- Liu, Y., Dolan, R. J., Kurth-Nelson, Z., and Behrens, T. E. (2019b). Human replay spontaneously reorganizes experience. *Cell*, 178(3):640–652.
- Liu, Y., Su, Y., Liu, A.-A., Schiele, B., and Sun, Q. (2020b). Mnemonics training: Multi-class incremental learning without forgetting. In *CVPR*, pages 12245–12254.
- Lopez-Paz, D. and Ranzato, M. (2017). Gradient episodic memory for continual learning. In *NeurIPS*, pages 6467–6476.
- Louie, K. and Wilson, M. A. (2001). Temporally Structured Replay of Awake Hippocampal Ensemble Activity during Rapid Eye Movement Sleep. *Neuron*, 29(1):145–156.

- Markram, H., Lübke, J., Frotscher, M., and Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic apss and epsps. *Science*, 275(5297):213–215.
- McClelland, J. L., McNaughton, B. L., and Lampinen, A. K. (2020). Integration of new information in memory: new insights from a complementary learning systems perspective. *Philosophical Transactions of the Royal Society B*, 375(1799):20190637.
- McClelland, J. L., McNaughton, B. L., and O’reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, page 419.
- McCloskey, M. and Cohen, N. J. (1989). Catastrophic interference in connectionist networks: The sequential learning problem. *Psychology of Learning and Motivation*, 24:109–165.
- McCormick, D. A. (1992). Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamocortical activity. *Progress in neurobiology*, 39(4):337–388.
- McDevitt, E. A., Duggan, K. A., and Mednick, S. C. (2015). REM sleep rescues learning from interference. *Neurobiology of Learning and Memory*, 122:51–62.
- McGaugh, J. L. (2000). Memory—a Century of Consolidation. *Science*, 287(5451):248–251.
- McNamara, C. G., Tejero-Cantero, Á., Trouche, S., Campo-Urriza, N., and Dupret, D. (2014). Dopaminergic neurons promote hippocampal reactivation and spatial memory persistence. *Nature neuroscience*, 17(12):1658–1660.
- Mnih, V., Kavukcuoglu, K., Silver, D., Graves, A., Antonoglou, I., Wierstra, D., and Riedmiller, M. (2013). Playing atari with deep reinforcement learning. *arXiv preprint arXiv:1312.5602*.
- Mnih, V., Kavukcuoglu, K., Silver, D., Rusu, A. A., Veness, J., Bellemare, M. G.,

- Graves, A., Riedmiller, M., Fidjeland, A. K., Ostrovski, G., et al. (2015). Human-level control through deep reinforcement learning. *Nature*, 518(7540):529.
- Mölle, M., Yeshenko, O., Marshall, L., Sara, S. J., and Born, J. (2006). Hippocampal sharp wave-ripples linked to slow oscillations in rat slow-wave sleep. *Journal of neurophysiology*.
- Momennejad, I. (2020). Learning Structures: Predictive Representations, Replay, and Generalization. *Current Opinion in Behavioral Sciences*, 32:155–166.
- Moore, A. W. and Atkeson, C. G. (1993). Prioritized sweeping: Reinforcement learning with less data and less time. *Machine learning*, 13(1):103–130.
- Morison, R. and Dempsey, E. (1941). A study of thalamo-cortical relations. *American Journal of Physiology-Legacy Content*, 135(2):281–292.
- Muller, L., Piantoni, G., Koller, D., Cash, S. S., Halgren, E., and Sejnowski, T. J. (2016). Rotating Waves during Human Sleep Spindles Organize Global Patterns of Activity That Repeat Precisely through the Night. *eLife*, 5:e17267.
- Nádasdy, Z., Hirase, H., Czurkó, A., Csicsvari, J., and Buzsáki, G. (1999). Replay and Time Compression of Recurring Spike Sequences in the Hippocampus. *The Journal of Neuroscience*, 19(21):9497–9507.
- Nadel, L. and Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, 7(2):217–227.
- Nguyen, C. V., Li, Y., Bui, T. D., and Turner, R. E. (2018). Variational continual learning. In *ICLR*.
- Nishida, M. and Walker, M. P. (2007). Daytime Naps, Motor Memory Consolidation and Regionally Specific Sleep Spindles. *PloS one*, 2(4):e341.
- O’Keefe, J. and Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Clarendon Press ; Oxford University Press, Oxford : New York.

- Ólafsdóttir, H. F., Barry, C., Saleem, A. B., Hassabis, D., and Spiers, H. J. (2015). Hippocampal place cells construct reward related sequences through unexplored space. *eLife*, 4:e06063.
- Ólafsdóttir, H. F., Bush, D., and Barry, C. (2018). The role of hippocampal replay in memory and planning. *Current Biology*, 28(1):R37–R50.
- Olcese, U., Esser, S. K., and Tononi, G. (2010). Sleep and synaptic renormalization: a computational study. *Journal of neurophysiology*, 104(6):3476–3493.
- O'Reilly, R. C. and Rudy, J. W. (2001). Conjunctive representations in learning and memory: principles of cortical and hippocampal function. *Psychological review*, 108(2):311.
- Ostapenko, O., Puskas, M., Klein, T., Jähnichen, P., and Nabi, M. (2019). Learning to remember: A synaptic plasticity driven framework for continual learning. In *CVPR*, pages 11321–11329.
- Ozdemir, F., Fuernstahl, P., and Goksel, O. (2018). Learn the new, keep the old: Extending pretrained models with new anatomy and images. In *International Conference on Medical Image Computing and Computer-Assisted Intervention*, pages 361–369. Springer.
- Ozdemir, F. and Goksel, O. (2019). Extending pretrained segmentation networks with additional anatomical structures. *International journal of computer assisted radiology and surgery*, 14(7):1187–1195.
- Parisi, G. I., Kemker, R., Part, J. L., Kanan, C., and Wermter, S. (2019). Continual lifelong learning with neural networks: A review. *Neural Networks*.
- Parisi, G. I., Tani, J., Weber, C., and Wermter, S. (2018). Lifelong learning of spatiotemporal representations with dual-memory recurrent self-organization. *Frontiers in Neurorobotics*, 12:78.
- Pavlides, C. and Winson, J. (1989). Influences of hippocampal place cell firing in the

- awake state on the activity of these cells during subsequent sleep episodes. *Journal of Neuroscience*, 9(8):2907–2918.
- Payne, J. D., Stickgold, R., Swanberg, K., and Kensinger, E. A. (2008). Sleep preferentially enhances memory for emotional components of scenes. *Psychological Science*, 19(8):781–788.
- Pellegrini, L., Graffieti, G., Lomonaco, V., and Maltoni, D. (2019). Latent replay for real-time continual learning. *arXiv preprint arXiv:1912.01100*.
- Peyrache, A., Khamassi, M., Benchenane, K., Wiener, S. I., and Battaglia, F. P. (2009). Replay of Rule-Learning Related Neural Patterns in the Prefrontal Cortex during Sleep. *Nature neuroscience*, 12(7):919–926.
- Pfeiffer, B. E. (2020). The content of hippocampal “replay”. *Hippocampus*, 30(1):6–18.
- Pfeiffer, B. E. and Foster, D. J. (2013). Hippocampal place-cell sequences depict future paths to remembered goals. *Nature*, 497(7447):74–79.
- Pritzel, A., Uria, B., Srinivasan, S., Badia, A. P., Vinyals, O., Hassabis, D., Wierstra, D., and Blundell, C. (2017). Neural episodic control. In *ICML*, pages 2827–2836. JMLR. org.
- Ramanathan, D. S., Gulati, T., and Ganguly, K. (2015). Sleep-Dependent Reactivation of Ensembles in Motor Cortex Promotes Skill Consolidation. *PLoS Biol*, 13(9):e1002263.
- Rasch, B. and Born, J. (2013). About Sleep’s Role in Memory. *Physiological reviews*, 93(2):681–766.
- Rebuffi, S.-A., Kolesnikov, A., Sperl, G., and Lampert, C. H. (2017). icarl: Incremental classifier and representation learning. In *CVPR*, pages 2001–2010.
- Riemer, M., Cases, I., Ajemian, R., Liu, M., Rish, I., Tu, Y., , and Tesauro, G. (2019). Learning to learn without forgetting by maximizing transfer and minimizing interference. In *ICLR*.

- Rios, A. and Itti, L. (2018). Closed-loop memory gan for continual learning. *arXiv preprint arXiv:1811.01146*.
- Ritter, H., Botev, A., and Barber, D. (2018). Online structured laplace approximations for overcoming catastrophic forgetting. In *NeurIPS*, pages 3738–3748.
- Robertson, E. M. and Genzel, L. (2020). Memories replayed: reactivating past successes and new dilemmas.
- Robins, A. (1995). Catastrophic forgetting, rehearsal and pseudorehearsal. *Connection Science*, 7(2):123–146.
- Ruder, S. (2017). An overview of multi-task learning in deep neural networks. *arXiv preprint arXiv:1706.05098*.
- Rusu, A. A., Rabinowitz, N. C., Desjardins, G., Soyer, H., Kirkpatrick, J., Kavukcuoglu, K., Pascanu, R., and Hadsell, R. (2016). Progressive neural networks. *arXiv:1606.04671*.
- Sanda, P., Malerba, P., Jiang, X., Krishnan, G. P., Gonzalez-Martinez, J., Halgren, E., and Bazhenov, M. (2021). Bidirectional interaction of hippocampal ripples and cortical slow waves leads to coordinated spiking activity during nrem sleep. *Cerebral Cortex*, 31(1):324–340.
- Schaul, T., Quan, J., Antonoglou, I., and Silver, D. (2016). Prioritized experience replay. In *ICLR*.
- Scheffer, T., Decomain, C., and Wrobel, S. (2001). Active hidden markov models for information extraction. In *International Symposium on Intelligent Data Analysis*, pages 309–318. Springer.
- Schmidhuber, J. (1991). Curious model-building control systems. In *Proc. international joint conference on neural networks*, pages 1458–1463.
- Schönauer, M., Geisler, T., and Gais, S. (2014). Strengthening Procedural Memories by Reactivation in Sleep. *Journal of Cognitive Neuroscience*, 26(1):143–153.

- Sejnowski, T. J. and Destexhe, A. (2000). Why do we sleep? Published on the World Wide Web on 7 November 2000. *Brain Research*, 886(1):208–223.
- Senghas, A., Kita, S., and Özyürek, A. (2004). Children creating core properties of language: Evidence from an emerging sign language in nicaragua. *Science*, 305(5691):1779–1782.
- Serra, J., Suris, D., Miron, M., and Karatzoglou, A. (2018). Overcoming catastrophic forgetting with hard attention to the task. In *ICML*, pages 4555–4564.
- Settles, B. (2009). Active learning literature survey. Technical report, University of Wisconsin-Madison Department of Computer Sciences.
- Shen, B. and McNaughton, B. L. (1996). Modeling the spontaneous reactivation of experience-specific hippocampal cell assemblies during sleep. *Hippocampus*, 6(6):685–692.
- Shin, H., Lee, J. K., Kim, J., and Kim, J. (2017). Continual learning with deep generative replay. In *NeurIPS*, pages 2990–2999.
- Siapas, A. G. and Wilson, M. A. (1998). Coordinated interactions between hippocampal ripples and cortical spindles during slow-wave sleep. *Neuron*, 21(5):1123–1128.
- Singer, A. C. and Frank, L. M. (2009). Rewarded outcomes enhance reactivation of experience in the hippocampus. *Neuron*, 64(6):910–921.
- Sirota, A., Csicsvari, J., Buhl, D., and Buzsáki, G. (2003). Communication between neocortex and hippocampus during sleep in rodents. *Proceedings of the National Academy of Sciences*, 100(4):2065–2069.
- Smith, C. and Smith, D. (2003). Ingestion of ethanol just prior to sleep onset impairs memory for procedural but not declarative tasks. *Sleep*, 26(2):185–191.
- Sodhani, S., Chandar, S., and Bengio, Y. (2020). Toward training recurrent neural networks for lifelong learning. *Neural computation*, 32(1):1–35.

- Standley, T., Zamir, A., Chen, D., Guibas, L., Malik, J., and Savarese, S. (2020). Which tasks should be learned together in multi-task learning? In *ICML*, pages 9120–9132.
- Staresina, B. P., Bergmann, T. O., Bonnefond, M., Van Der Meij, R., Jensen, O., Deuker, L., Elger, C. E., Axmacher, N., and Fell, J. (2015). Hierarchical nesting of slow oscillations, spindles and ripples in the human hippocampus during sleep. *Nature neuroscience*, 18(11):1679–1686.
- Stella, F., Baracska, P., O’Neill, J., and Csicsvari, J. (2019). Hippocampal reactivation of random trajectories resembling brownian diffusion. *Neuron*, 102(2):450–461.
- Steriade, M., Nunez, A., and Amzica, F. (1993). A novel slow (≈ 1 Hz) oscillation of neocortical neurons in vivo: depolarizing and hyperpolarizing components. *Journal of neuroscience*, 13(8):3252–3265.
- Steriade, M., Timofeev, I., and Grenier, F. (2001). Natural waking and sleep states: a view from inside neocortical neurons. *Journal of neurophysiology*, 85(5):1969–1985.
- Stickgold, R. (2005). Sleep-Dependent Memory Consolidation. *Nature*, 437(7063):1272–1278.
- Stickgold, R. (2012). To Sleep: Perchance to Learn. *Nature neuroscience*, 15(10):1322–1323.
- Stickgold, R., Scott, L., Rittenhouse, C., and Hobson, J. A. (1999). Sleep-induced changes in associative memory. *Journal of cognitive neuroscience*, 11(2):182–193.
- Tadros, T., Krishnan, G., Ramyaa, R., and Bazhenov, M. (2020a). Biologically inspired sleep algorithm for increased generalization and adversarial robustness in deep neural networks. In *ICLR*.
- Tadros, T., Krishnan, G., Ramyaa, R., and Bazhenov, M. (2020b). Biologically inspired sleep algorithm for reducing catastrophic forgetting in neural networks. In *AAAI*, pages 13933–13934.
- Tao, X., Chang, X., Hong, X., Wei, X., and Gong, Y. (2020). Topology-preserving class-incremental learning. In *ECCV*, pages 254–270.

- Tasar, O., Tarabalka, Y., and Alliez, P. (2019). Incremental learning for semantic segmentation of large-scale remote sensing data. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 12(9):3524–3537.
- Tatsuno, M., Lipa, P., and McNaughton, B. L. (2006). Methodological Considerations on the Use of Template Matching to Study Long-Lasting Memory Trace Replay. *Journal of Neuroscience*, 26(42):10727–10742.
- Teyler, T. J. and Rudy, J. W. (2007). The hippocampal indexing theory and episodic memory: Updating the index. *Hippocampus*, 17(12):1158–1169.
- Tibon, R., Gronau, N., Scheuplein, A.-L., Mecklinger, A., and Levy, D. A. (2014). Associative recognition processes are modulated by the semantic unitizability of memoranda. *Brain and Cognition*, 92:19–31.
- Tingley, D. and Peyrache, A. (2020). On the methods for reactivation and replay analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1799):20190231.
- Titsias, M. K., Schwarz, J., de G. Matthews, A. G., Pascanu, R., and Teh, Y. W. (2020). Functional regularisation for continual learning with gaussian processes. In *ICLR*.
- Tononi, G. and Cirelli, C. (2014). Sleep and the Price of Plasticity: From Synaptic and Cellular Homeostasis to Memory Consolidation and Integration. *Neuron*, 81(1):12–34.
- van de Ven, G. M., Siegelmann, H. T., and Tolias, A. S. (2020). Brain-inspired replay for continual learning with artificial neural networks. *Nature communications*, 11(1):1–14.
- Van Hasselt, H., Guez, A., and Silver, D. (2016). Deep reinforcement learning with double q-learning. In *AAAI*, pages 2094–2100.
- von Oswald, J., Henning, C., Sacramento, J., and Grewe, B. F. (2020). Continual learning with hypernetworks. In *ICLR*.

- Wagner, U., Gais, S., and Born, J. (2001). Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep. *Learning & memory*, 8(2):112–119.
- Wagner, U., Gais, S., Haider, H., Verleger, R., and Born, J. (2004). Sleep inspires insight. *Nature*, 427(6972):352–355.
- Walker, M., Stickgold, R., Alsop, D., Gaab, N., and Schlaug, G. (2005). Sleep-Dependent Motor Memory Plasticity in the Human Brain. *Neuroscience*, 133(4):911–917.
- Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., and Stickgold, R. (2002a). Practice with Sleep Makes Perfect: Sleep-Dependent Motor Skill Learning. *Neuron*, 35(1):205–211.
- Walker, M. P., Liston, C., Hobson, J. A., and Stickgold, R. (2002b). Cognitive flexibility across the sleep–wake cycle: Rem-sleep enhancement of anagram problem solving. *Cognitive Brain Research*, 14(3):317–324.
- Walker, M. P. and Stickgold, R. (2004). Sleep-dependent learning and memory consolidation. *Neuron*, 44(1):121–133.
- Walker, M. P. and Stickgold, R. (2010). Overnight alchemy: sleep-dependent memory evolution. *Nature Reviews Neuroscience*, 11(3):218.
- Wang, K., Zhang, D., Li, Y., Zhang, R., and Lin, L. (2016). Cost-effective active learning for deep image classification. *IEEE Transactions on Circuits and Systems for Video Technology*, 27(12):2591–2600.
- Watson, C. J., Baghdoyan, H. A., and Lydic, R. (2010). Neuropharmacology of Sleep and Wakefulness. *Sleep medicine clinics*, 5(4):513–528.
- Wei, K., Iyer, R., and Bilmes, J. (2015). Submodularity in data subset selection and active learning. In *ICML*, pages 1954–1963.

- Wei, Y., Krishnan, G. P., and Bazhenov, M. (2016). Synaptic Mechanisms of Memory Consolidation during Sleep Slow Oscillations. *The Journal of Neuroscience*, 36(15):4231–4247.
- Wei, Y., Krishnan, G. P., Komarov, M., and Bazhenov, M. (2018). Differential roles of sleep spindles and sleep slow oscillations in memory consolidation. *PLOS Computational Biology*, 14(7):e1006322.
- Wilson, M. A. and McNaughton, B. L. (1994). Reactivation of hippocampal ensemble memories during sleep. *Science*, 265(5172):676–679.
- Wu, C., Herranz, L., Liu, X., Wang, Y., van de Weijer, J., and Raducanu, B. (2018). Memory replay gans: learning to generate images from new categories without forgetting. In *NeurIPS*, pages 5966–5976.
- Wu, Y., Chen, Y., Wang, L., Ye, Y., Liu, Z., Guo, Y., and Fu, Y. (2019a). Large scale incremental learning. In *CVPR*, pages 374–382.
- Wu, Z., Wang, X., Gonzalez, J. E., Goldstein, T., and Davis, L. S. (2019b). Ace: Adapting to changing environments for semantic segmentation. In *ICCV*, pages 2121–2130.
- Ye, F. and Bors, A. G. (2020). Learning latent representations across multiple data domains using lifelong vaegan. In *ECCV*, pages 777–795.
- Yoo, D. and So Kweon, I. (2019). Learning loss for active learning. In *CVPR*, pages 93–102.
- Yoon, J., Yang, E., Lee, J., and Hwang, S. J. (2018). Lifelong learning with dynamically expandable networks. In *ICLR*.
- Yu, J. Y., Kay, K., Liu, D. F., Grossrubatscher, I., Loback, A., Sosa, M., Chung, J. E., Karlsson, M. P., Larkin, M. C., and Frank, L. M. (2017). Distinct hippocampal-cortical memory representations for experiences associated with movement versus immobility. *eLife*, 6:e27621.

- Yu, J. Y., Liu, D. F., Loback, A., Grossrubatscher, I., and Frank, L. M. (2018). Specific hippocampal representations are linked to generalized cortical representations in memory. *Nature Communications*, 9(1):2209.
- Zenke, F., Poole, B., and Ganguli, S. (2017). Continual learning through synaptic intelligence. In *ICML*, pages 3987–3995.
- Zhang, Y. and Yang, Q. (2017). A survey on multi-task learning. *arXiv preprint arXiv:1707.08114*.
- Zhao, B., Xiao, X., Gan, G., Zhang, B., and Xia, S.-T. (2020). Maintaining discrimination and fairness in class incremental learning. In *CVPR*, pages 13208–13217.
- Zhou, T. and Bilmes, J. (2018). Minimax curriculum learning: Machine teaching with desirable difficulties and scheduled diversity. In *ICLR*.